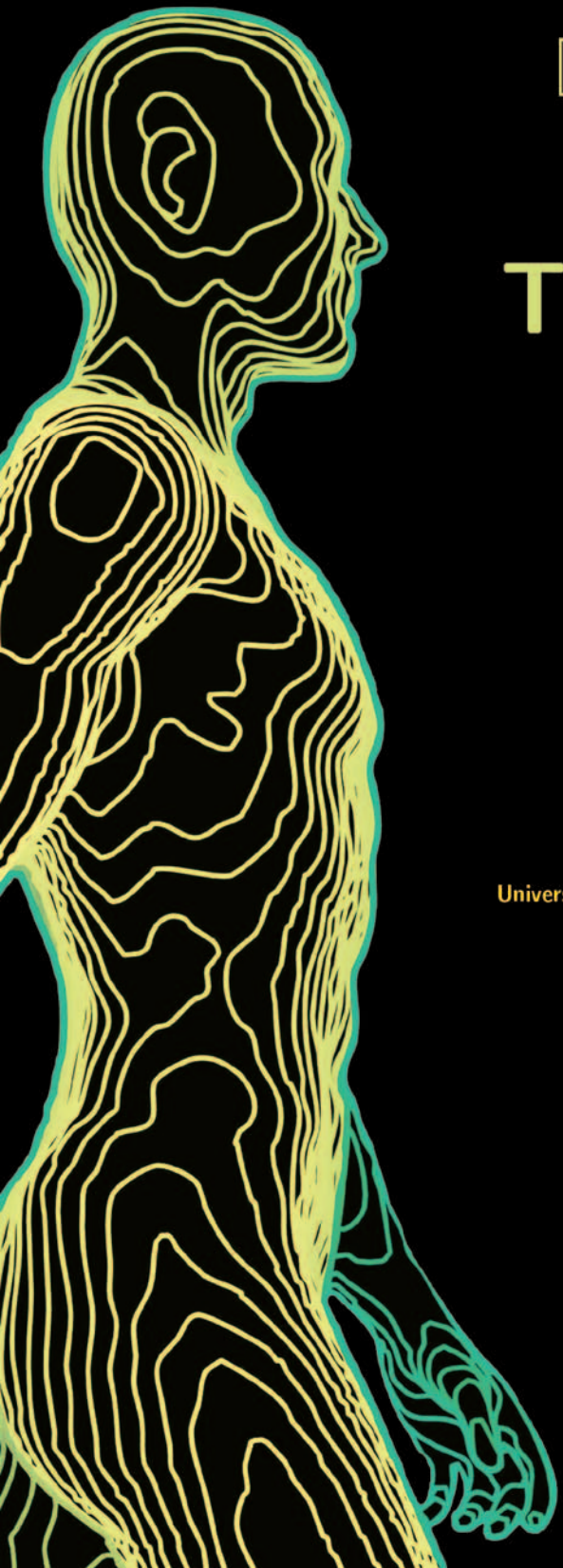

YOUR BODY How It Works

The Senses

Douglas Light

INTRODUCTION
Denton A. Cooley, M.D.
President & Surgeon-in-Chief
of the Texas Heart Institute
Clinical Professor of Surgery at the
University of Texas Medical School, Houston, Texas

YOUR BODY
How It Works

The Senses

YOUR BODY How It Works

Cells, Tissues, and Skin

The Circulatory System

Digestion and Nutrition

The Endocrine System

Human Development

The Immune System

The Nervous System

The Reproductive System

The Respiratory System

The Senses

The Skeletal and Muscular Systems

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CHELSEA HOUSE
PUBLISHERS
A Haights Cross Communications Company
Philadelphia

The Senses

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Chelsea House
An imprint of Infobase Publishing
132 West 31st Street
New York NY 10001

ISBN-10: 0-7910-7908-2
ISBN-13: 978-0-7910-7908-9

Library of Congress Cataloging-in-Publication Data
Light, Douglas B., 1956–
The senses / Douglas B. Light; introduction by Denton A. Cooley.
p. cm.—(Your body, how it works)
Includes bibliographical references and index.
ISBN 0-7910-7908-2
1. Senses and sensation. I. Title. II. Series.
QP431.L546 2004
612.8—dc22 2004014295

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You can find Chelsea House on the World Wide Web at
http://www.chelseahouse.com

Text and cover design by Terry Mallon

Printed in the United States of America

Bang 21C 10 9 8 7 6 5 4 3 2

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Introduction

The human body is an incredibly complex and amazing structure. At best, it is a source of strength, beauty, and wonder. We can compare the healthy body to a well-designed machine whose parts work smoothly together. We can also compare it to a symphony orchestra in which each instrument has a different part to play. When all of the musicians play together, they produce beautiful music.

From a purely physical standpoint, our bodies are made mainly of water. We are also made of many minerals, including calcium, phosphorous, potassium, sulfur, sodium, chlorine, magnesium, and iron. In order of size, the elements of the body are organized into cells, tissues, and organs. Related organs are combined into systems, including the musculoskeletal, cardiovascular, nervous, respiratory, gastrointestinal, endocrine, and reproductive systems.

Our cells and tissues are constantly wearing out and being replaced without our even knowing it. In fact, much of the time, we take the body for granted. When it is working properly, we tend to ignore it. Although the heart beats about 100,000 times per day and we breathe more than 10 million times per year, we do not normally think about these things. When something goes wrong, however, our bodies tell us through pain and other symptoms. In fact, pain is a very effective alarm system that lets us know the body needs attention. If the pain does not go away, we may need to see a doctor. Even without medical help, the body has an amazing ability to heal itself. If we cut ourselves, the blood clotting system works to seal the cut right away, and

the immune defense system sends out special blood cells that are programmed to heal the area.

During the past 50 years, doctors have gained the ability to repair or replace almost every part of the body. In my own field of cardiovascular surgery, we are able to open the heart and repair its valves, arteries, chambers, and connections. In many cases, these repairs can be done through a tiny "keyhole" incision that speeds up patient recovery and leaves hardly any scar. If the entire heart is diseased, we can replace it altogether, either with a donor heart or with a mechanical device. In the future, the use of mechanical hearts will probably be common in patients who would otherwise die of heart disease.

Until the mid-twentieth century, infections and contagious diseases related to viruses and bacteria were the most common causes of death. Even a simple scratch could become infected and lead to death from "blood poisoning." After penicillin and other antibiotics became available in the 1930s and '40s, doctors were able to treat blood poisoning, tuberculosis, pneumonia, and many other bacterial diseases. Also, the introduction of modern vaccines allowed us to prevent childhood illnesses, smallpox, polio, flu, and other contagions that used to kill or cripple thousands.

Today, plagues such as the "Spanish flu" epidemic of 1918–19, which killed 20 to 40 million people worldwide, are unknown except in history books. Now that these diseases can be avoided, people are living long enough to have long-term (chronic) conditions such as cancer, heart failure, diabetes, and arthritis. Because chronic diseases tend to involve many organ systems or even the whole body, they cannot always be cured with surgery. These days, researchers are doing a lot of work at the cellular level, trying to find the underlying causes of chronic illnesses. Scientists recently finished mapping the human genome,

which is a set of coded "instructions" programmed into our cells. Each cell contains 3 billion "letters" of this code. By showing how the body is made, the human genome will help researchers prevent and treat disease at its source, within the cells themselves.

The body's long-term health depends on many factors, called risk factors. Some risk factors, including our age, sex, and family history of certain diseases, are beyond our control. Other important risk factors include our lifestyle, behavior, and environment. Our modern lifestyle offers many advantages but is not always good for our bodies. In western Europe and the United States, we tend to be stressed, overweight, and out of shape. Many of us have unhealthy habits such as smoking cigarettes, abusing alcohol, or using drugs. Our air, water, and food often contain hazardous chemicals and industrial waste products. Fortunately, we can do something about most of these risk factors. At any age, the most important things we can do for our bodies are to eat right, exercise regularly, get enough sleep, and refuse to smoke, overuse alcohol, or use addictive drugs. We can also help clean up our environment. These simple steps will lower our chances of getting cancer, heart disease, or other serious disorders.

These days, thanks to the Internet and other forms of media coverage, people are more aware of health-related matters. The average person knows more about the human body than ever before. Patients want to understand their medical conditions and treatment options. They want to play a more active role, along with their doctors, in making medical decisions and in taking care of their own health.

I encourage you to learn as much as you can about your body and to treat your body well. These things may not seem too important to you now, while you are young, but the habits and behaviors that you practice today will affect your

physical well-being for the rest of your life. The present book series, YOUR BODY: HOW IT WORKS, is an excellent introduction to human biology and anatomy. I hope that it will awaken within you a lifelong interest in these subjects.

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1

Sensory Receptors and Sensation

The human brain is truly an amazing organ. Although it only weighs about 1.4 kilograms (3 lbs), this highly organized collection of cells lets us communicate with others, perform mental tasks, remember homework assignments, understand concepts, be aware of our surroundings, and move our body parts. However, the brain would be useless without its connections to the outside world. In fact, as strange as it sounds, we do not experience our environment and the events taking place within our bodies directly or in their entirety. Instead, we experience them by way of specialized sense organs that send information to our brain. In other words, just about everything we know about the world comes to us through our senses, and everything we do depends on receiving and correctly interpreting information from our external and internal environments.

SENSATION AND PERCEPTION

Both sensation and perception are functions of the brain—specifically, a part of the brain called the **cerebral cortex**, or cerebrum (Figure 1.1). Nerve impulses that go to the brain are called sensations. A **sensation** is defined as the awareness and localization of a **stimulus**, a change in the internal or external environment that leads to a response. Once our brain is aware of sensations, it interprets them, letting us perceive a stimulus. A **perception**, therefore, involves giving meaning to a sensation based on what we have experienced and

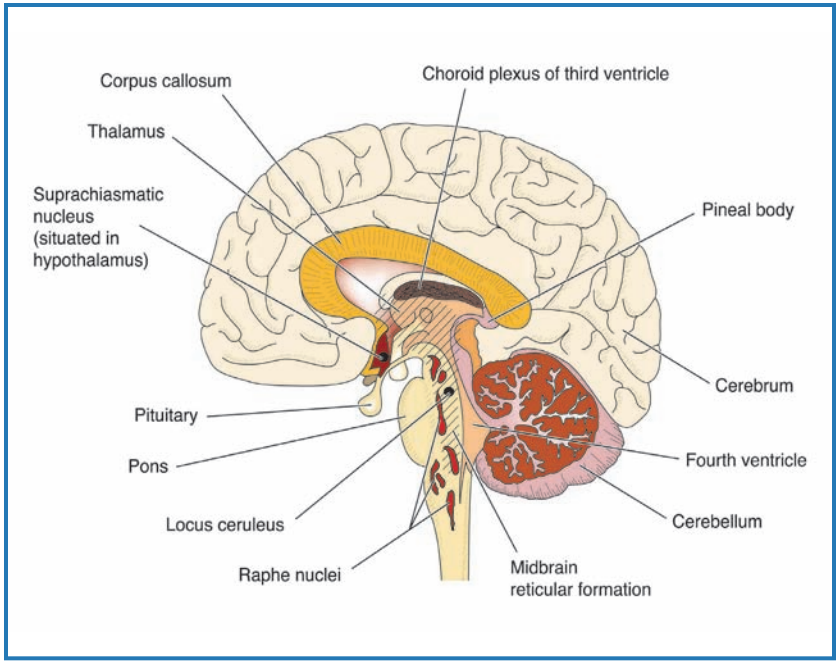

Figure 1.1 **This illustration shows a view of the right side of the human brain, with all of the parts that work together to help us understand our environment. Each half of the brain has a cerebral cortex (cerebrum), a layer of gray matter about 2 to 4 millimeters (1/8 inch) thick. It is in the cerebrum that the brain identifies and interprets sensations.**

learned. For instance, stepping on a tack will cause a sensation of pain, whereas an awareness of being injured would be considered a perception. Perception is important in determining how we will respond to a particular stimulus.

THE ROLE OF SENSORY RECEPTORS

Sensations, and the perceptions they evoke, begin with **sensory reception**, the detection of a stimulus (or, more accurately, the energy of a stimulus) by sensory receptors. **Sensory receptors** are anatomical structures made up of special cells that respond to specific changes in their environment (stimuli). In so doing, they provide the central nervous system (brain and spinal cord) with information about conditions both inside

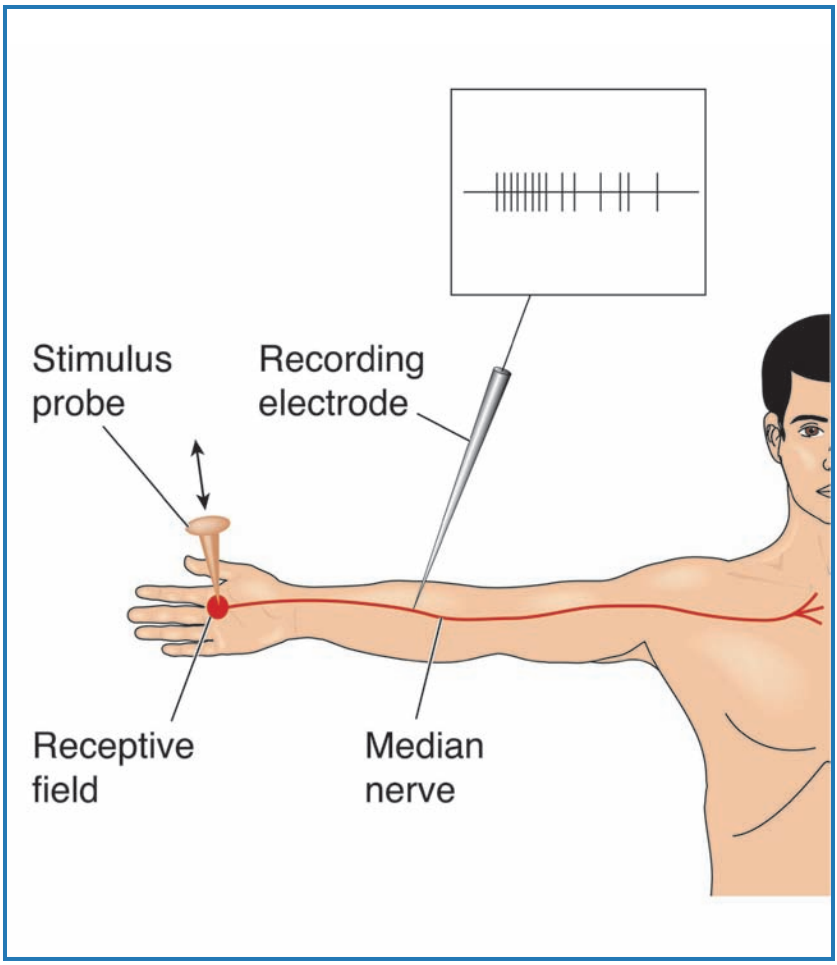

Figure 1.2 Scientists have different ways to test human sensory receptors. A researcher may probe a person's hand with an electrical signal to stimulate it and record how often parts of the brain send and receive signals about the sensation. The median nerve of the arm (seen in this diagram) is the pathway that brings the signal from the sensory receptors of the hand to the brain.

and outside the body. In this way, sensory receptors are the physical links between your central nervous system and the environment (Figure 1.2).

TRANSDUCTION AND RECEPTOR POTENTIALS

Sensory receptors work by first detecting a stimulus and then translating that energy into electrical signals, which are conducted by nerve cells, or **neurons**, to the central nervous system. Turning a stimulus into an electrical signal is called **transduction** (a transducer is a device that changes one form of energy into another). Sensory receptors have to be present to detect (and then perceive) stimuli because the brain has no such ability of its own. The brain is designed to receive electrical signals from the nervous system; beyond that, it is essentially "blind" to all other forms of stimuli.

The initial response of a sensory receptor to a stimulus is to change its cell membrane permeability to ions—how many ions it lets through. In other words, in response to an appropriate stimulus, transport pathways for specific ions open and/or close, depending on the type of stimulus and receptor (Figure 1.3).

DID YOU KNOW?

Sensory organs are the only channels of communication between the brain and the outside world. Simply put, the brain is not designed to sense on its own. For instance, an exposed brain would neither sense light shining on it nor feel something touching it. In fact, patients are often kept awake during brain surgery, which can help a surgeon isolate specific regions of the brain. The ancient Greek philosopher Aristotle recognized this characteristic of the brain over 2,000 years ago when he said, "Nothing is in the mind that does not pass through the senses." This concept can be seen clearly when volunteers are blindfolded and placed in the warm water of a sensory deprivation tank. They soon experience visual, auditory, and tactile (touch) hallucinations, as well as incoherent thought patterns. From these experiments and others, it is apparent that we need constant input from our senses to carry out functions that give us personality and intellect.

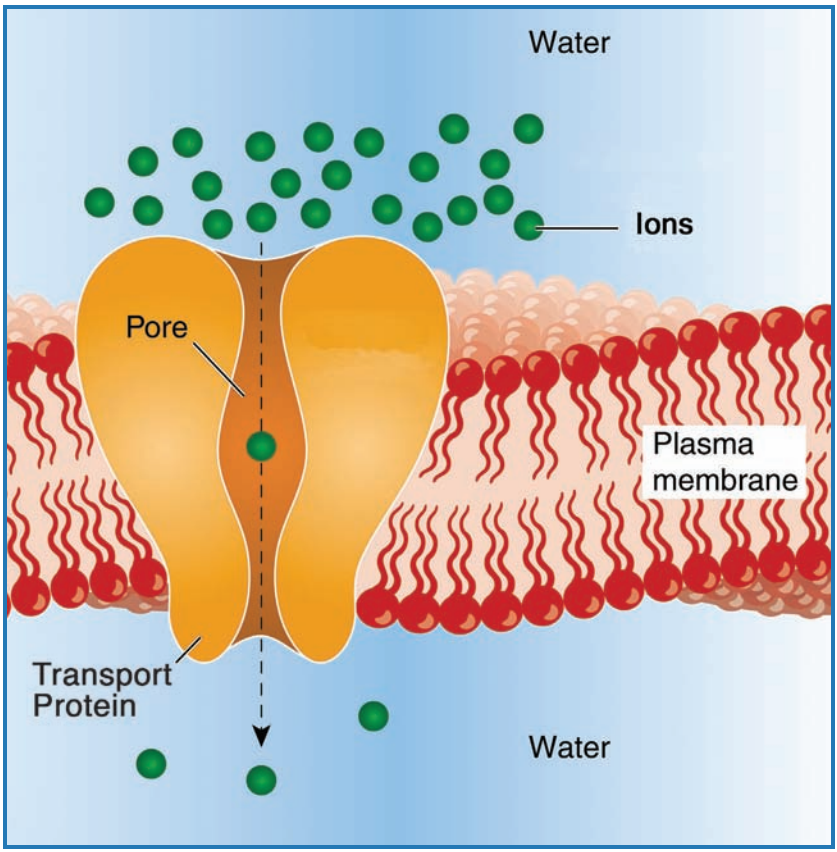

Figure 1.3 **Sensory receptors respond to stimuli by changing their cell membrane to let in or keep out electrically charged ions. They do this with the help of transport proteins—chemicals that create pores that allow ions into the cell membrane, as seen in this diagram.**

This, in turn, influences the movement of a charge across the cell membrane, resulting in a graded change in the membrane potential (voltage), which is called a **receptor potential**. The magnitude of a receptor potential is directly related to how strong the stimulus is. If a receptor potential is large enough, it may result in a conscious sensation by the brain (that is, a conscious awareness of the stimulus). However, much of the

sensory information that goes to the central nervous system is filtered out by specific parts of the brain; as a result, no sensation is perceived for many stimuli. This is important because the brain would otherwise be overloaded with too many signals to sort through. For instance, we usually are not aware of our muscle tension or blood pH levels. We also have the ability to listen to a friend in a noisy restaurant, while simultaneously "tuning out" the myriad other conversations and sounds around us.

SENSORY MODALITY AND RECEPTOR SPECIFICITY

We are able to distinguish a variety of sensory stimuli because each kind of stimulus activates different types of receptor cells. The term **modality** refers to the type of sensation a stimulus produces. That is, each category of sensation—such as touch, taste, or sound—is a sensory modality. The features that characterize stimuli within a certain modality are called qualities. For instance, light can be red or blue, taste can be sweet or sour, and sounds can be high or low in pitch.

Each receptor has its own special sensitivity to stimuli. For example, a receptor for light does not react to sound waves, and a taste receptor that responds to dissolved chemicals does not respond to light. This concept of receptors responding only to a particular stimulus is called **receptor specificity**. Interestingly, and amazingly, many receptors can detect the smallest physical unit of stimulus possible. For example, some receptor cells of the nose can detect a single molecule of odor! The receptor cells of the inner ear can sense motion of only a few angstroms (about the size of a single water molecule), and many photoreceptor cells can detect a single quantum (photon) of light.

Receptors can be categorized in different ways based on:

(1) the type of sensation (modality) to which they respond,

(2) the location of the stimulus to which they respond, and

(3) their structural complexity, whether they are simple or complicated.

CLASSIFICATION OF RECEPTORS BY MODALITY

Receptors that respond to chemicals in solution are called **chemoreceptors**. Some chemoreceptors are general receptors that detect information about the total number of dissolved substances in a solution. For instance, **osmoreceptors** in your brain are chemoreceptors that sense changes in the total solute (dissolved substances) concentration of the blood and make you thirsty when this concentration increases. In contrast, other types of chemoreceptors respond to individual kinds of molecules. The stimulus molecule binds to a specific site on the membrane of the receptor cell, which leads to changes in membrane permeability and alters the membrane potential. These kinds of chemoreceptors are involved with taste and smell.

Receptors that respond to light are called **photoreceptors**. The eye contains two kinds of photoreceptors: rods (for vision in dim light) and cones (for color vision). **Thermoreceptors** are sensitive to temperature changes, and react to either heat or cold. The body, in turn, uses this information to regulate both its surface and core (internal) temperature. Receptors that are stimulated by touch, pressure, stretch, tension, or vibration are called **mechanoreceptors**. These include receptors in the organs for hearing and balance (located in the inner ear) and many receptors in the skin, viscera (internal organs), and joints. Muscle spindle fibers are specialized mechanoreceptors, called stretch receptors, that monitor the length of skeletal muscles.

Receptors that respond to potentially damaging stimuli and cause pain are called **nociceptors**. Stimuli that influence

nociceptors include trauma from blows or cuts, ischemia (poor blood flow), and too much stimulation by heat, radiation, and chemicals. Although, for some people, chronic pain can be debilitating, the sensation of pain is necessary for survival because the stimulus that causes pain often translates into a defensive reaction or withdrawal from danger. Imagine how difficult it would be for you to survive if you lacked the ability to sense pain. Without a sense of pain, you wouldn't know when you should, for example, pull your hand away from a hot stove or a sharp knife.

CLASSIFICATION OF RECEPTORS BY LOCATION

Receptors may also be classified according to the location of the stimulus to which they respond. Receptors that detect stimuli that come from inside the body, such as those from the internal organs and blood vessels, are called **interoceptors**. They monitor a variety of stimuli, including chemical changes in body fluids, tissue stretch, and body temperature. Although we are usually unaware of the workings of interoceptors, they sometimes can produce feelings of visceral pain, nausea, stretch, pressure, hunger, or thirst. **Exteroceptors**, on the other

DID YOU KNOW?

You can reduce the perception of pain if you take certain drugs. Two common over-the-counter analgesics (painkillers) are aspirin and ibuprofen. They decrease pain by inhibiting the body's production of chemicals called prostaglandins, which cause pain and inflammation by making receptors more sensitive. Thus, aspirin and ibuprofen essentially lower the number of signals that go to the brain from pain receptors. In contrast, the much stronger drug morphine acts directly on receptors in the brain so that incoming signals are not sensed and perceived at all.

hand, respond to stimuli coming from outside the body. They include receptors for touch, pressure, pain, temperature, vision, hearing, taste, and smell. **Proprioceptors** are located in skeletal muscles, tendons, and joints, and in the ligaments and connective tissue that cover the bones and muscles. They are important for sensing the position and movements of the body and its parts.

CLASSIFICATION OF RECEPTORS BY STRUCTURAL COMPLEXITY

Another way to classify receptors is by how complex their structure is. The majority of receptors are considered **simple receptors**, which means that they are made up of the modified endings (called **dendrites**) of **sensory neurons** (nerves that send signals from receptors to the central nervous system—the brain and spinal cord). Simple receptors are found throughout the body and monitor most types of **general senses**, which include tactile sensation (touch, pressure, stretch, and vibration), temperature monitoring (heat and cold), and pain. In contrast, **complex receptors** are those we think of as the classical **sense organs**: localized collections of cells associated with the **special senses** (hearing, balance, smell, vision, and taste).

SENSORY RECEPTOR TRANSMISSION

Sensory receptors transmit four kinds of information: modality, location, intensity, and duration. As stated previously, modality is the type of sensation produced by a stimulus, such as vision, hearing, or taste. However, nerve impulses that reach the brain from virtually all kinds of receptors are identical in nature. How, then, does the brain distinguish between different modalities if the input it receives is the same from all receptors? It does this by having nerve impulses arrive via different nerve fibers, which, in turn, stimulate different centers in the brain. This arrangement is referred to as a **labeled line code**. In essence, the brain has a number of "lines" (nerve fibers) that

deliver information. These might be compared to phone lines. Just as each phone line handles a different conversation, each nerve fiber represents a specific modality. In other words, even though all the nerve impulses arriving in the brain are similar in nature (all are electrical signals), the impulses that arrive on one nerve fiber have a different meaning from impulses arriving on another. For instance, any nerve impulses that go to the brain from the optic nerve are interpreted as light. This helps explain why a blow to the eye, which can stimulate the optic nerve, may initially be perceived as a flash of light rather than pain. Imagine what would happen to perception if the nerve fibers leaving receptors were somehow mixed up before they arrived at the brain.

The location of a stimulus is encoded by the specific nerve fibers that are firing. That is, the brain has the ability to tell where the stimulus is coming from based on information carried by nerve fibers, which is termed **sensory projection**. Sometimes the brain can be fooled, however. One example is **phantom pain**—the perception of a feeling of pain in a limb after it has been surgically amputated. Phantom pain demonstrates that sensory projection is a process that occurs in the brain—not at the level of the receptor. The brain also can determine how intense a stimulus is based on the number and kinds of nerve fibers that are firing and also on the amount of time between stimuli.

RECEPTOR ADAPTATION

Many types of receptors have the ability to change their frequency of firing over time in response to a constant stimulus. This process, called **adaptation**, refers to a decrease in responsiveness of receptors during continued stimulation. **Phasic receptors** generate a burst of activity when they are first stimulated and then quickly stop transmitting impulses even if the stimulus continues (in other words, they adapt quickly). Tactile receptors in the skin and hair receptors are two examples of rapidly adapting phasic receptors. If these receptors

were not phasic, we would sense a continual barrage of stimuli. For instance, without sensory adaptation, you would feel every bit of clothing on your body all day long.

In contrast to phasic receptors, **tonic receptors** adapt slowly and therefore generate nerve impulses continually. Proprioceptors—receptors located in skeletal muscles, tendons, and joints—are among the most slowly adapting tonic receptors. This is significant because the brain must always be aware of body position, muscle tension, and joint motions.

CONNECTIONS

A sensation is the awareness and localization of a stimulus (a change in the internal or external environment that evokes a response). Once the brain is aware of sensations, it interprets them, helping us perceive what the stimulus is. Sensations and the perceptions they evoke begin with sensory reception, the detection of a stimulus by sensory cells and its transduction into an electrical signal. We are able to tell different types of sensory stimuli apart because they selectively activate different specialized types of receptor cells.

Receptors that respond to chemicals in solution are called chemoreceptors, whereas those that respond to light energy are known as photoreceptors. Thermoreceptors are sensitive to temperature changes, and those that are stimulated by physical deformation are called mechanoreceptors. Nociceptors respond to potentially damaging stimuli and cause pain.

Receptors that detect stimuli arising from within the body are called interoceptors. They monitor a variety of stimuli, including chemical changes in body fluids, tissue stretch, and body temperature. In contrast, exteroceptors respond to stimuli coming from outside the body, and proprioceptors are located in skeletal muscles, tendons, and joints.

Sensory receptors transmit four kinds of information: modality, location, intensity, and duration. This is accomplished,

in part, by having nerve impulses arrive in the brain via different nerve fibers, thereby stimulating different brain centers. This arrangement is termed a labeled line code.

Receptors can change how often they fire over time in response to a constant stimulus. This process is called adaptation, and it refers to a decrease in the responsiveness of receptors during continued stimulation. Phasic receptors generate a burst of activity when first stimulated, then quickly stop sending impulses even if the stimulus is still going on. In contrast, tonic receptors adapt slowly and therefore generate nerve impulses continually.

2

The General Senses

The receptors for the general senses are scattered throughout the body and are relatively simple in structure. They consist of one or a few sensory nerve fibers and usually a sparse amount of connective tissue that enhances their sensitivity or how specific their responses are. The general sensory receptors are involved in tactile sensation (touch, pressure, stretch, and vibration), temperature monitoring (heat and cold), and pain, as well as muscle tension and joint position. They can be classified according to whether they have unencapsulated or capsulated nerve endings.

UNENCAPSULATED NERVE ENDINGS

Unencapsulated nerve endings are nerve endings that are not wrapped in connective tissue. They are found nearly everywhere in the body, but are especially abundant in epithelial tissues (such as skin) and tissues that hold body parts together (such as tendons and muscles). Most of these sensory nerves are fibers that are small in diameter and have no special association with accessory cells or tissues, although their ends usually have small, knob-like swellings. Among this type of sensory nerves are warm receptors, which respond to rising temperatures; cold receptors, which respond to falling temperatures; and nociceptors, which sense pain.

Some unencapsulated nerve endings are associated with enlarged, disk-shaped epidermal (skin) cells (called Merkel cells) and form

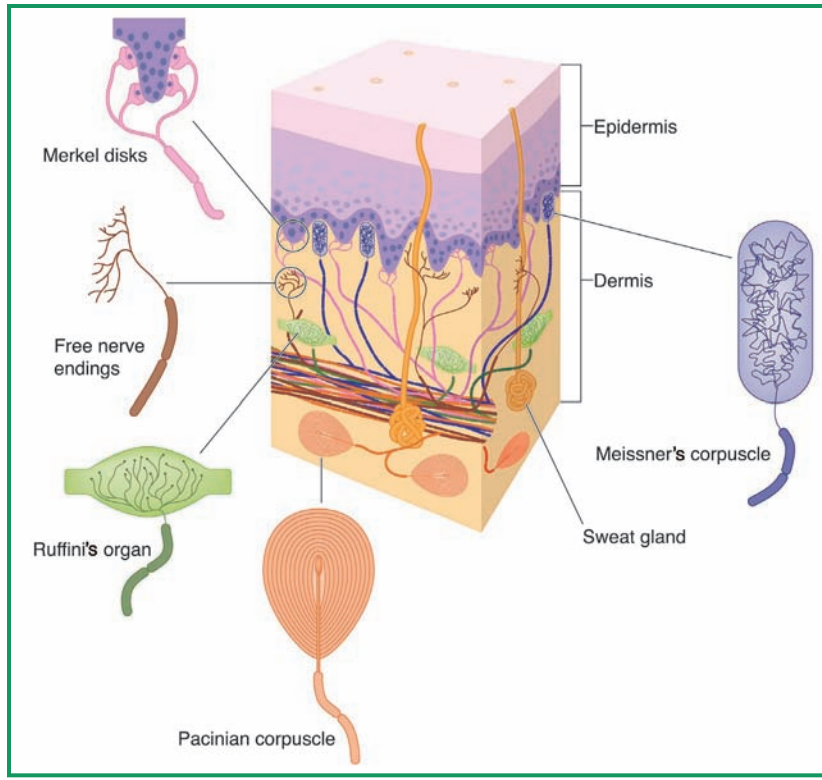

Figure 2.1 **This three-dimensional view of skin reveals why the surface of our body is sensitive to a variety of stimuli. Skin contains various cells that help us sense our environment. Merkel disks, Meissner's corpuscles, and Ruffini's organs (or corpuscles), for example, sense light touches and pressure, while Pacinian corpuscles sense vibration.**

Merkel disks, which lie in the deep layers of the skin's epidermis, the outermost layer of the skin (Figure 2.1). These structures are tonic receptors for light touch and are thought to help us sense different textures, edges, and shapes.

Other free nerve endings, called **root hair plexuses**, monitor the movement of hairs by wrapping around hair follicles. They respond to any light touch that bends a hair. For instance, when a mosquito lands on your skin or an ant crawls on the back of your neck, they bend hairs, and this is detected by root hair plexuses. Because this type of receptor adapts quickly, we are

not constantly aware of our clothing, even though it continually bends our body hairs.

Some unencapsulated nerve endings branch within the walls of organs that can expand (called "elastic" walls), such as blood vessels or parts of the digestive, urinary, and respiratory tracts. These nerve endings monitor changes in pressure. They are called **baroreceptors** (Figure 2.2). These receptors respond immediately to changes in pressure, but they also adapt rapidly. Baroreceptors are especially important for regulating blood pressure, and are found in the walls of major blood vessels, such as the carotid artery (which delivers oxygen-rich blood to the brain) and the aorta (the major artery exiting the heart). Baroreceptors in the digestive system provide information on the volume of organs and also trigger reflexes that move materials through the digestive tract. Similarly, stretch receptors in the wall of the urinary bladder give us information about the volume of the bladder and also are involved with triggering urination. Baroreceptors in the lungs monitor the degree of lung expansion and help prevent the lungs from stretching too much. They also help regulate the smooth rhythm of breathing.

As mentioned earlier, some unencapsulated nerve endings detect small changes in the concentration of specific chemicals; they are called chemoreceptors. Chemoreceptors do not send information to the primary sensory cortex of the brain, so we are not consciously aware of the sensations they provide. Instead, their signals go to parts of the brain that deal with **autonomic** (unconscious) control over breathing and cardiovascular functions. Some important chemoreceptors are located in the aorta and in the carotid bodies, structures near the origin of the carotid artery. These particular chemoreceptors monitor levels of carbon dioxide and hydrogen ions (acid) in the blood, which helps the brain control how fast and how deeply we breathe. There also are chemoreceptors in the brain that respond to levels of acid in the cerebrospinal fluid, the liquid that fills the spaces in and around the brain and spinal cord.

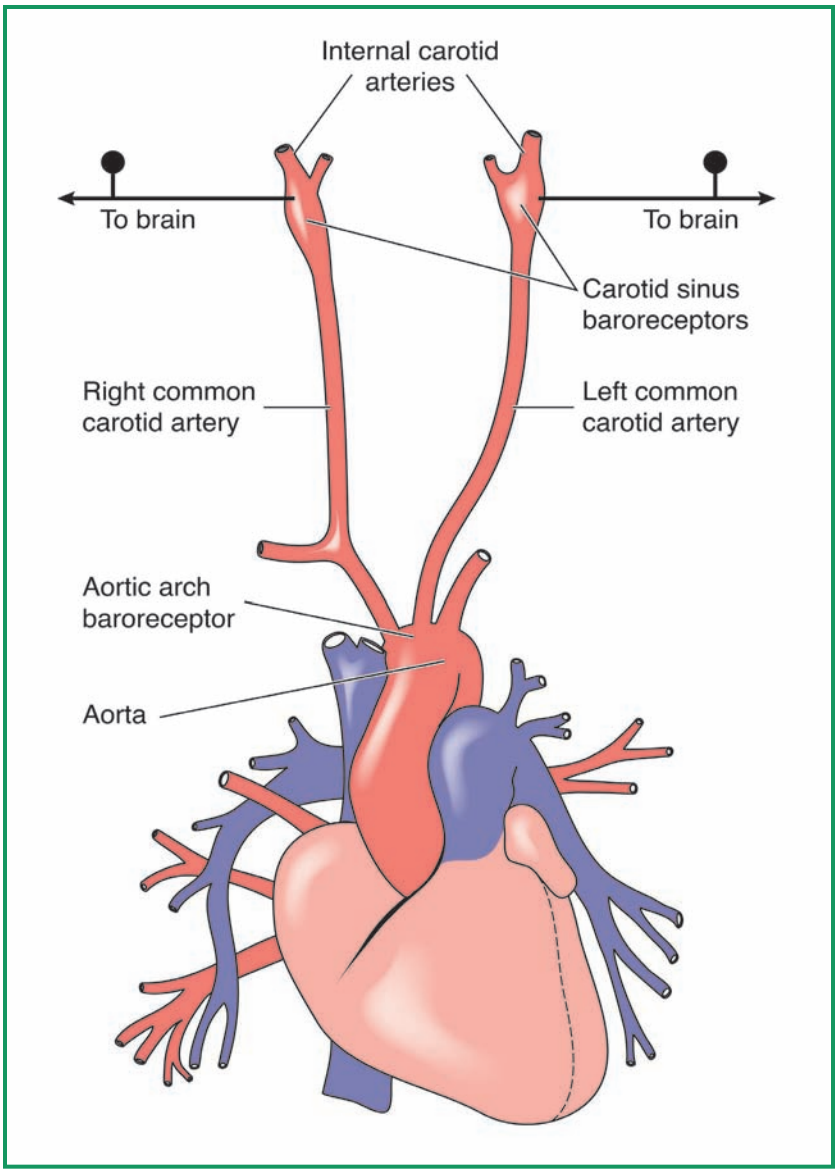

Figure 2.2 Baroreceptors are found in the carotid sinus and aortic arch. When the blood pressure in the arteries rises and stretches these receptors, they send a rapid stream of signals to the central nervous system. This leads the blood vessels to become wider, which lowers blood pressure.

ENCAPSULATED NERVE ENDINGS

All **encapsulated nerve endings** consist of one or more fiber terminals (nerve endings) of sensory nerves that are wrapped in special connective tissue, which enhances the sensitivity and specificity of the receptor. Virtually all of these receptors are mechanoreceptors for touch, pressure, and stretch. However, they vary in shape, size, and distribution in the body.

Meissner's corpuscles are phasic receptors for light touch and texture (refer again to Figure 2.1). They are found just beneath the skin epidermis in the **dermal papillae**, and are especially numerous in sensitive and hairless skin areas, such as the fingertips, palms of the hands, soles of the feet, eyelids, lips, nipples, and genitals. They are oval in shape and fairly large, about 100 micrometers (μM) long and 50 μM wide. The dendrites of these cells are highly coiled and are

DID YOU KNOW?

Unencapsulated nerve endings are responsible, at least in part, for itch and tickle sensations. Itch receptors consist of unencapsulated nerve endings located in the dermis, the inner layer of the skin. There are many of them inside the surfaces of the eyelids and the mucous membranes of the nose. However, there are no itch sensations in other mucous membranes or in deep tissues and viscera (internal organs). Itch receptors can be directly stimulated by certain chemicals, such as histamine and other agents released by white blood cells during inflammation. This explains why the administration of an antihistamine or cortisone, agents that stop white blood cells from releasing some chemicals, helps make inflamed areas less itchy.

Tickle sensations are produced by a light touch that moves across the skin and are probably caused by the stimulation of itch receptors. Psychological factors (such as the person's mood) are also involved in the perception of tickle sensations. Different people have very different levels of tickle sensitivity. This is why some people are so much more "ticklish" than others.

surrounded by modified **Schwann cells**, a type of cell that forms insulation around nerve fibers. A fibrous capsule wraps around the entire complex, which anchors it within the dermis.

Meissner's corpuscles are sensitive to fine touch and pressure, as well as to low-frequency vibration. They enable us to tell the difference between a smooth texture, such as silk, and a rough surface, like sandpaper. Tactile receptors play essentially the same role in light touch reception in hairless skin that the root hair plexuses play in hairy skin. Meissner's corpuscles adapt quickly to stimulation, usually within just one second after contact. **Krause end bulbs** are similar to Meissner's corpuscles in their sensitivity to touch, but they are found in mucous membranes rather than in the skin.

Pacinian corpuscles are phasic receptors for deep pressure, stretch, tickle, and vibration (refer back to Figure 2.1). They are scattered in the dermis of the skin and in the tissue beneath it, and are especially numerous in the hands, feet, breasts, and genitals. Pacinian corpuscles consist of a single nerve ending surrounded by up to 60 concentric layers of connective tissue. In cross-section, they look something like a sliced onion. They are the largest of the corpuscular receptors, and may reach 3 to 4 millimeters (mm) in length and 1 mm in diameter (large enough to be seen with the naked eye). The concentric layers shield the dendrite from virtually all sources of stimulation other than direct pressure. Although these receptors are stimulated by deep pressure, they respond only when a stimulus is first applied, and then they quickly adapt. Thus, Pacinian corpuscles are best suited to sense vibrations.

Ruffini's corpuscles are tonic receptors for heavy touch, pressure, stretching of the skin, and joint movements (refer again to Figure 2.1). They lie beneath the skin and inside ligaments, tendons, and joints, and respond to deep and continuous pressure. They look like long, flattened capsules containing a few nerve fibers intertwined with collagen fibers. Any tension or distortion of the dermis tugs and twists the capsular fibers,

stretching or squeezing the attached dendrites, which leads to a change in their membrane potential. Ruffini's corpuscles are tonic receptors and show little adaptation.

Muscle spindles are proprioceptors found throughout skeletal muscles. Each muscle spindle is a bundle of 3 to 10 modified skeletal muscle fibers, called intrafusal fibers, enclosed within a connective tissue capsule. These intrafusal fibers are about one-fourth the diameter of normal muscle fibers, which are called extrafusal fibers. The central region of an intrafusal fiber lacks the ability to contract. Instead, these structures act as receptive surfaces, since they are wrapped with sensory nerves that lead to the central nervous system. In this way, intrafusal fibers can tell when a muscle stretches and then respond by initiating a reflex that resists further stretch.

Golgi tendon organs are proprioceptors found in tendons, close to the point where a tendon fuses with a skeletal muscle. They consist of small bundles of collagen fibers enclosed in a layered capsule, with dendrites coiling between and around the fibers (structurally, they look like Ruffini's corpuscles). Golgi tendon organs help regulate the length of skeletal muscles by monitoring the tension produced when muscles contract; they are stimulated when a muscle contracts and stretches a tendon. This, in turn, prevents the tearing or breaking of tendons.

PAIN RECEPTION

Pain is not just an annoying sensation; it makes us aware of tissue injuries, so we can try to protect the injured region, giving the injury a better chance to heal. It also lets us know about potentially hazardous situations, enabling us to avoid injury in the first place. Pain is not simply due to an over-stimulation of other receptors. Instead, it has its own set of receptors—nociceptors—that have large receptive fields (which may make it difficult to determine the exact source of a painful sensation). Nociceptors are especially common in

the skin and mucous membranes, joint capsules, the outer lining of bones, and around the walls of blood vessels. There also are some nociceptors located in deep tissues and in most of the visceral organs. However, there are no nociceptors in the brain.

There are two types of nociceptors. Some nociceptors belong to nerves that are surrounded by a **myelin sheath**, an insulating layer made up of Schwann cells. This sheath allows these nerves to conduct signals at rapid speeds, up to 80 m/sec (250 ft/sec). Consequently, they produce the sensation known as **fast pain**. We feel this as sharp, localized, stabbing pain perceived at the time of injury. In contrast, nociceptors that are part of nerves without a myelin sheath send their signals at much slower speeds, from 0.5 to 2.0 m/sec. These receptors are responsible for **slow pain**—a longer-lasting, dull, diffuse feeling.

Pain is classified by its point of origin. **Somatic pain** arises from the skin, muscles, or joints. It can be either superficial or deep. Superficial somatic pain is a sharp, stabbing, pricking

DID YOU KNOW?

As mentioned earlier, pain plays an important role in survival because it makes us aware when parts of our body get injured. Without pain, we would ignore simple cuts and splinters, which could lead to more serious infections. A good example of the protective function of pain is seen in people with leprosy (Hansen's disease). This condition is caused by a bacterium that infects nerves, resulting in a loss of pain and other sensations in the affected areas. As a result, victims often fail to notice minor injuries, such as scrapes, cuts, splinters, and burns. Neglecting these wounds leads to serious infections that damage deep tissue, including bone. In fact, it is common for people with leprosy to be forced to have some of their fingers and toes amputated because minor injuries have progressed to the point of developing necrosis (tissue death).

pain that often causes us to cry out. It is transmitted to the brain by myelinated fibers—fibers encased in a myelin sheath—and is usually brief and localized to the skin epidermis and mucous membranes. In contrast, deep somatic pain is less localized, longer-lasting, and more likely to be experienced as burning, itching, or aching. It results from stimulation of pain receptors in the deep skin layers, muscles, or joints, and indicates that tissue destruction is occurring. Deep somatic pain signals are sent to the brain by unmyelinated fibers.

Visceral pain results from noxious (harmful) stimulation of receptors in the organs of the thorax and abdominal cavity. Like deep somatic pain, it usually consists of a dull ache or a burning feeling, and often includes nausea. Although it may be intense, it is poorly localized because the viscera themselves have relatively few nociceptors. Visceral pain arises from extreme stretching of tissues, chemical irritants, muscle spasms, or **ischemia** (deficient blood flow).

Because visceral pain inputs to the central nervous system follow the same pathways as somatic pain, the brain may perceive visceral pain as somatic in origin. This phenomenon is known as **referred pain** (Figure 2.3). For example, people who suffer heart attacks often feel the pain that is really coming from the heart as if it were radiating along the left shoulder and left arm. Because the skin has more pain receptors than the heart and experiences injuries far more often, the brain assumes that signals arriving on that labeled line are coming from the skin, even when the heart is the actual source. That is why it is important for doctors to know about referred pain and which internal organs link to other body parts so they can better diagnose an organ dysfunction.

CONNECTIONS

Unencapsulated nerve endings are not wrapped in connective tissue and are found nearly everywhere in the body. Merkel disks, which lie in the deeper layers of the skin epidermis, are

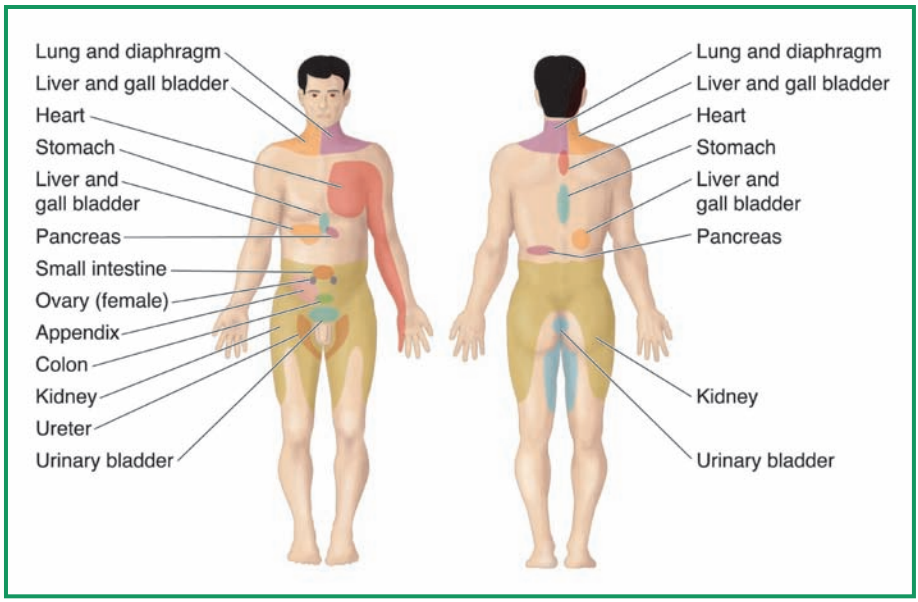

Figure 2.3 **When internal organs experience pain, they send signals to the brain along the same pathways that other body parts, such as skin and muscles, use. Since the body and skin feel pain much more often than organs do, the brain may perceive the pain as coming from skin or muscle, rather than from the organ that is actually in pain. This phenomenon is called "referred pain." This diagram shows which internal organs the brain often confuses with particular body parts when they are in pain.**

tonic receptors for light touch. Other unencapsulated nerve endings, called root hair plexuses, monitor the movement of hairs by wrapping around hair follicles.

Some free nerve endings, called baroreceptors, are especially important for monitoring blood pressure, providing information on the volume of organs, moving materials through the digestive tract, causing urination, and regulating the expansion of the lungs. Chemoreceptors detect small changes in the concentration of specific chemicals.

Encapsulated nerve endings consist of one or more fiber terminals of sensory nerves enclosed in a connective tissue

capsule, which enhances the sensitivity and specificity of the receptor. Virtually all of these receptors are mechanoreceptors for touch, pressure, and stretch. Meissner's corpuscles, phasic receptors for light touch and texture, are found just beneath the skin epidermis in the dermal papillae. These tactile receptors are sensitive to fine touch and pressure, as well as to low-frequency vibrations. Krause end bulbs are similar to Meissner's corpuscles in terms of their sensitivity to touch, but they are found in mucous membranes. Pacinian corpuscles are phasic receptors for deep pressure, stretch, tickle, and vibration. They are scattered in the dermis of the skin and in the tissue under it. These receptors are best at monitoring vibration. Ruffini's corpuscles are tonic receptors for heavy touch, pressure, stretching of the skin, and joint movements. They lie deep within the skin and in subcutaneous (under the skin) tissue, ligaments, tendons, and joint capsules, and respond to deep and continuous pressure. Ruffini's corpuscles show little adaptation.

Muscle spindles are proprioceptors found throughout skeletal muscles. They contain intrafusal fibers enclosed within a connective tissue capsule, and act as receptive surfaces by

DID YOU KNOW?

We all have the same physical threshold for pain. That is, different people's receptors all respond to painful stimuli at the same intensity. For example, we sense heat as painful at 111° to 115°F (44° to 46°C), the range at which it begins to damage tissue. However, our reactions to pain, or pain tolerance, vary widely and are influenced by cultural, emotional, and psychological factors. This is why someone involved in a disaster may feel no pain while struggling to save him- or herself or others, even if he or she actually has severe injuries. In some cultures, like India, for example, people sometimes walk over hot coals to demonstrate their mastery over pain. Interestingly, pain tolerance seems to increase with age.

being wrapped with sensory nerves that lead to the central nervous system. In this way, intrafusal fibers detect muscle stretch and cause a reflex that resists further stretch. Golgi tendon organs are proprioceptors located in tendons. They help regulate the length of skeletal muscles by monitoring the tension produced when muscles contract.

Nociceptors are unencapsulated nerve endings with large receptive fields, and are especially common in the skin and mucous membranes, joint capsules, the outer lining of bones, and around the walls of blood vessels. Some nociceptors belong to nerves that are surrounded by a myelin sheath, an insulating layer made of Schwann cells. This sheath allows the nerves to conduct signals at rapid speeds and produce the sensation known as fast pain. In contrast, nociceptors that are part of nerves without a myelin sheath conduct at much slower speeds and are responsible for slow pain—a longer-lasting, dull, diffuse feeling.

Pain is also classified by its point of origin. Somatic pain arises from the skin, muscles, or joints. Visceral pain results from noxious stimulation of receptors in the organs of the thorax and abdominal cavity. Because sensations of visceral pain follow the same pathways as somatic pain, projection by the brain may cause visceral pain to be perceived as somatic in origin, a phenomenon known as referred pain.

3

Sense of Taste

Gustation, the sense of taste, is conducted by chemoreceptors that respond to chemicals dissolved in watery solution in our mouths. Gustation is important because it provides information about the quality of the food and liquid that we consume. Most important, it helps us determine whether the items we place in our mouths should be swallowed or rejected. In fact, the word *taste* comes from the Latin word *taxare*, which means "to feel," "touch," or "judge," which suggests that *taste* originally meant to test by touching.

LOCATION OF TASTE RECEPTORS

The receptor organs for gustation are called **taste buds**, which are structures composed of specialized epithelial cells. Taste buds are found in the mouth, with most of them located on the superior (top) surface of the tongue. However, a few taste buds are also found in the pharynx (throat), soft palate, and epiglottis. As we age, these nonlingual (non-tongue) taste buds decrease in number and importance.

The tongue has epithelial folds and bumps called **lingual papillae**, peg-like projections that give the tongue a slightly rough feel (Figure 3.1). There are four types of lingual papillae on the human tongue; only three of these have taste buds. **Foliate papillae** are arranged as closely packed folds along the back edges of the tongue. They are well developed in children, but are much less prominent and numerous in adults. In fact, most of these taste buds degenerate by the time a person is 2 or 3 years old. **Fungiform papillae** are mushroom-shaped structures. They are the only

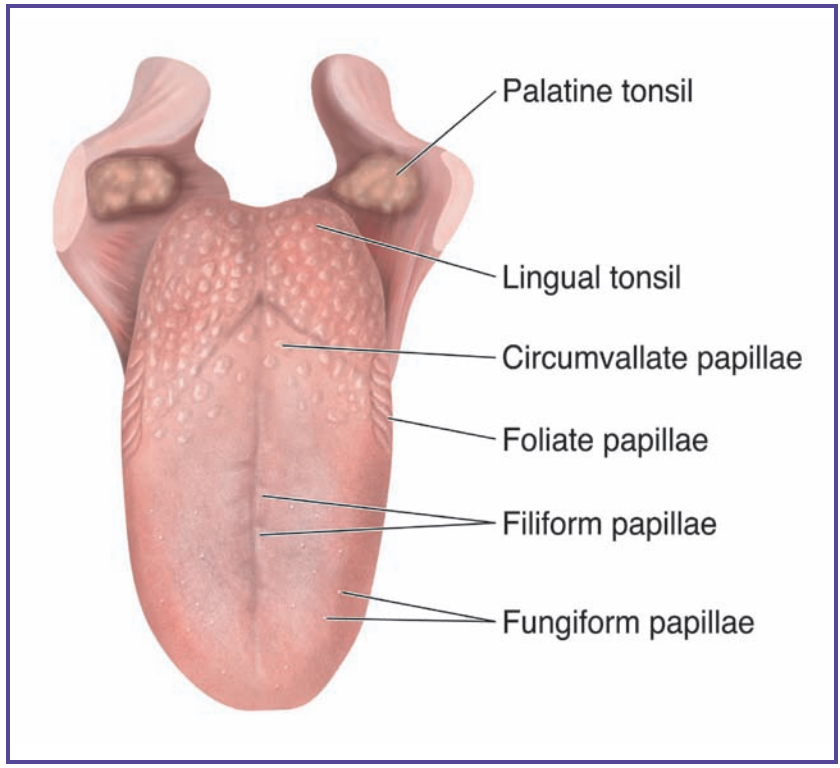

Figure 3.1 **The papillae look like tiny pegs standing up on the surface of the tongue. There are several kinds of papillae (shown here), some of which have taste buds—the receptors for the sense of gustation.**

papillae scattered over the entire surface of the tongue (they are most numerous at the tip and sides of the tongue). These papillae usually contain two to five taste buds, which are located on their outer surface. **Circumvallate papillae** are the largest papillae in size, and each contains about 250 taste buds. Humans typically have 7 to 12 circumvallate papillae, arranged in the shape of an upside down "V" at the back of the tongue. **Filiform papillae** look like tiny bumps that cover the surface of the tongue. Although they are the most numerous papillae, they play no sensory role because they have no taste buds. They are especially prominent (and rough) in cats. Many mammals use them to groom their fur.

Embedded in the connective tissue below the circumvallate and foliate papillae are **serous glands**. These glands have ducts that open into the depressions between adjacent papillae and between papillae and the wall of the tongue. Their secretions wash away particles of food and microorganisms. The presence of these secretions helps lower the concentration of substances that stimulate the taste buds.

TASTE BUDS

Regardless of location, all taste buds have a similar structure and look alike. Each one consists of 40 to 100 epithelial cells, and is about 50 micrometers (μM) in diameter. Taste buds are composed of three major cell types: sensory cells, basal cells, and supporting cells.

One kind of sensory cell is the **gustatory cell**—a slender, banana-shaped cell that bears microscopic hairs (microvilli). These microvilli are called **taste hairs** and are covered with taste receptors. During chewing, water-soluble substances from food dissolve in saliva and enter a **taste pore** of the gustatory cell. There, they contact the taste receptors of the microvilli. Interestingly, the sensory cells (the taste receptors in this case) are not neurons; they are epithelial cells that synapse (connect) with nerve fibers at their base. These nerve fibers then send a signal to the brain that lets it know a particular substance is present.

Despite being located within a protective pore, gustatory cells are still subject to a lot of damage from friction and from hot foods. Consequently, a typical gustatory cell only lives about 7 to 10 days. Gustatory cells are continually replaced by nearby **basal cells**, which divide and then turn into new supporting cells and gustatory cells. During the changeover, the connection between the nerve fibers and old gustatory cells must be disrupted, and new synapses formed. Finally, **supporting cells**, which are found between gustatory cells, provide support to the taste buds. They are the majority cell type and help insulate sensory cells.

Although supporting cells are shaped like gustatory cells, they lack taste hairs.

TASTE SENSATIONS

When an individual's taste is tested with pure chemicals, five distinct sensations or qualities are detected: sweet, salty, sour, bitter, and umami. A sweet taste is produced by many organic compounds, especially sugars, as well as by some alcohols and amino acids. Unfortunately, the salts in lead paint have a sweet taste, which explains why young children are sometimes tempted to eat peeling paint. Sweetness is associated with foods high in caloric value and helps satisfy our need for carbohydrates and some amino acids. Saccharin, an artificial sweetener, tastes about 700 times sweeter than sucrose (table sugar), which is why it provides the sensation of sweetness without calories. Fructose (fruit sugar) also tastes sweeter than sucrose and is often added to soft drinks and colas to enhance their sweetness. Interestingly, many plants have evolved sweet nectar and fruits to entice animals to eat them, thereby dispersing their pollen and seeds.

Sour taste is usually associated with acids, especially with hydrogen ions (H^+) in solution. Citrus fruits often taste sour because they contain citric acid, which releases H^+ when dissolved in saliva. Taste for sour is beneficial because many sour, naturally acidic foods, such as citrus fruits, are excellent sources of vitamins and minerals.

Salty sensations are produced by metal ions, such as sodium (Na^+) and potassium (K^+). These ions are important electrolytes for body fluids, which explains why there is value in our ability to taste them.

Spoiled foods, alkaloids (such as caffeine, nicotine, quinine, and morphine), and some non-alkaloids (like aspirin) have a bitter taste. It is advantageous for us to be able to taste bitter items because these substances are often poisonous. In fact, a bitter sensation often makes us reject the item we

ingested. However, many vegetables, such as broccoli and tofu, contain bitter chemicals that actually act as anticancer agents. A number of people develop a taste for these and other bitter foods, such as olives and quinine water. Interestingly, although fruits and nectar are sweet, the leaves of many plants contain bitter, toxic alkaloids. This makes sense because it is not advantageous for plants to have their leaves eaten.

A fifth sensation, umami (a Japanese word for "delicious"), was recently discovered and is now considered a primary taste sensation. Umami is a pleasant taste elicited by amino acids, such as glutamate and aspartate, and by some small peptides and nucleotides. It is responsible for the "beef taste" of steak or beef broth. Umami also enhances other taste qualities, which is why monosodium glutamate (MSG), with its umami taste, is often used as a food additive or flavor enhancer. However, glutamate also is an excitatory neurotransmitter in the central nervous system. For this reason, some people are sensitive to MSG and respond by getting headaches and feeling flushed and dizzy when they eat it. Because MSG is often used in Chinese foods, sensitivity to it is sometimes called "Chinese restaurant syndrome."

In addition to the five basic qualities of taste described above, there are two accessory taste qualities: alkaline and metallic. An alkaline (soapy) sensation is produced by stimulation with potassium carbonate (potash). Some metals and metal salts have a specific metallic taste. Finally, although most people say that water has no taste, there are, in fact, water taste receptors in the pharynx. Signals from these receptors are processed by the hypothalamus of the brain and, in turn, affect body water balance and the regulation of blood volume.

SENSORY MAP OF THE TONGUE

There are no visible structural differences between taste buds in different areas of the tongue. However, sensory maps of the tongue developed in the early 20th century (as a result of misinterpreted data reported in the late 1800s) have been

commonly reproduced in textbooks. These maps indicate that there are regional differences in primary sensitivity; that is, they show that certain regions of the tongue are more sensitive to one kind of taste than to others. For instance, the tip of the tongue is noted for being most sensitive to sweet tastes, whereas the sides of the tongue are more sensitive to salty and sour tastes. The back of the tongue is said to be especially sensitive to bitter substances, which tend to trigger a rejection response, such as gagging, to protect against the ingestion of poisons and toxins. In fact, the threshold for bitter taste is the lowest of all tastes, meaning that we can taste lower concentrations of alkaloids than of sugars, acids, and salts. However, it should be noted that although taste maps are common in scientific literature, in reality, all taste buds respond to all taste qualities, and all primary tastes can be detected by all areas of the tongue that contain taste buds. In fact, there is no evidence that the specific taste sensitivities of certain tongue areas affect the way we perceive different taste qualities. In addition, some substances may change their flavor as they move through the mouth. For instance, saccharin is initially tasted as sweet on the tip of the tongue, but develops a bitter aftertaste at the back of the tongue.

Interestingly, mixing different qualities of tastes is not like mixing different colors of paint or light. For instance, when blue and yellow paints are mixed, the color green is produced, and there is no longer any indication of the two original colors. In contrast, when different tastes are mixed, each individual taste can still be detected. Lemonade, for example, simultaneously tastes both sweet and sour because it contains sugar and citric acid. Our ability to discriminate and combine different tastes is the essence of fine cooking, and chefs mix various combinations of spices to bring out different taste sensations.

People differ in how sensitive they are to taste. Some aspects of these individual differences can be inherited. In some

biology classes, students test their taste sensitivity with paper strips containing phenylthiourea (also known as phenylthiocarbamide or PTC). It turns out that approximately 70% of Caucasians can taste PTC (this ability is inherited as a dominant trait), whereas the other 30% are unable to detect it (this is inherited as a recessive trait). In addition, there are age-related changes in taste discrimination. The number of

DID YOU KNOW?

While eating food, the mouth is exposed to a number of different kinds of stimuli. For instance, because the mouth is in direct communication with the nose, volatile substances readily go from the mouth to odor receptors in the nose and give us the sensation of smell. In fact, most of what we perceive as taste involves the sense of smell. This helps explain why food tastes bland when your nose is stuffed up from a cold or allergy. In addition, anyone who has walked into a coffeehouse knows that the aroma of coffee is quite strong. However, without the sense of smell, coffee would lose its appeal and would simply taste bitter. Similarly, without smell, cinnamon would have only a faintly sweet taste.

The mouth also contains thermoreceptors, mechanoreceptors, and nociceptors, which are usually stimulated when we eat. In fact, "taste" is really a mixture of sensations: Odor, temperature, texture, and possibly pain are superimposed on the real taste sensations of sweet, salty, sour, bitter, and umami. For instance, thermoreceptors are involved when we say that lukewarm coffee tastes lousy, but piping hot coffee tastes great. Mechanoreceptors provide information about the texture of food, which is why some people say they don't like their green beans soft and mushy or don't like onions because they feel slimy. For some individuals, nociceptors need to be stimulated with chemicals found in hot chili peppers for food to "taste" good.

taste buds dramatically decreases by around age 50. Most humans are born with about 10,000 taste buds, but may die with as few as 2,000 to 4,000. This helps explain why elderly people may find some foods bland and unappetizing, whereas children may find the same foods too spicy or pungent.

Finally, there can be functional problems that interfere with taste. Many of these disturbances result from diseases, such as brain tumors. For instance, **hypogeusia** is a condition where the threshold (minimum concentration) for taste perception is above the normal range. It is harder for people with this condition to taste substances than it is for most people. Individuals with **ageusia** have no sense of taste at all. **Dysgeusia** refers to a distortion of taste in which the sensations experienced are usually unpleasant and do not correspond to the stimulus or result without any stimulus.

SIGNAL TRANSDUCTION DURING TASTE

For someone to be able to taste a chemical, the chemical must first dissolve in saliva and enter a taste pore. After contacting a taste hair, the chemical can set off an electrical change in the membrane of a sensory cell. This, in turn, causes a sensory cell to release specific chemicals that are stored in membranous sacs called vesicles found beneath the plasma membrane. These chemicals then bind to receptors on associated sensory nerve dendrites, which causes a change in the potential (voltage) across the nerve cell membrane. If this change is large enough, a signal is sent to the brain for interpretation.

There are still a number of unanswered questions concerning taste, especially with regard to relaying information to the central nervous system. For instance, taste signals sent to the brain do not represent a single taste modality. In other words, a single nerve leaving the tongue may send signals in response to both sour and salty tastes or both sour and bitter tastes. Thus, a single taste bud can respond to more than one kind of stimulant. This makes it unclear how distinct taste

sensations are coded. It is possible that single nerve fibers from the tongue, even though they respond to more than one type of taste, can have distinct preferences, with some responding best to sugar, others to salt, and others to acid. Perhaps these fibers serve as labeled lines that signal distinct taste sensations. Or, a perception of taste may occur only from the comparison of the activity of a large population of nerve fibers. The answers to these questions remain to be found.

CONNECTIONS

The sense of taste (gustation) is controlled by chemoreceptors that respond to chemicals dissolved in a watery solution on our tongues. Gustation is important because it provides information about the quality of the foods and liquids we consume. The sensory receptor organs for gustation are called taste buds, which are structures composed of specialized epithelial cells.

The tongue has epithelial projections or folds called lingual papillae, which are peg-like bumps. There are four types of lingual papillae that differ in distribution and structure; only three of them bear taste buds. Foliate papillae are arranged as closely packed folds along the back edges of the tongue. Fungiform papillae are mushroom-shaped and are the only papillae scattered over the entire surface of the tongue. They usually contain two to five taste buds located on the top surface. Circumvallate papillae are the largest in size; each contains about 250 taste buds. Filiform papillae are tiny bumps that cover the tongue. Although they are the most numerous papillae, they play no sensory role because they lack taste buds.

Taste buds are made up of 40 to 150 epithelial cells. There are three major types. Gustatory cells are slender cells that have taste hairs (microvilli). Water-soluble substances that reach the surface of the tongue can move through a taste pore into a fluid-filled space over the taste bud. A typical gustatory cell only lives about 7 to 10 days, and these cells are continually

replaced as nearby basal cells divide and turn into new sensory cells. Supporting cells, found between sensory cells, support the taste buds. These supporting cells are the most common type of taste bud. They lack taste hairs and help insulate gustatory cells.

Humans are able to detect five distinct taste sensations or qualities: sweet, salty, sour, bitter, and umami. A sweet taste is produced by many organic compounds, especially sugars and some amino acids. Sour is associated with acids, particularly with hydrogen ions (H^+). Salty sensations are produced by metal ions, such as sodium (Na^+) and potassium (K^+). Bitter tastes come from spoiled foods, alkaloids, and some non-alkaloids (such as aspirin). A fifth sensation, umami, is a pleasant taste produced by amino acids, such as glutamate and aspartate. It is responsible for the "beef taste" of steak.

Sensory maps of the tongue indicate that there are slight regional differences in primary sensitivity. The tip of the tongue is most sensitive to sweet tastes, whereas the sides of the tongue are more sensitive to salty and sour tastes, and the back of the tongue is especially sensitive to bitter substances. Although taste maps are common in scientific literature, it is important to remember that all taste buds respond to most, if not all, taste qualities.

The perception of taste is a sensation that depends on many factors, including the sense of smell (chemoreceptors), as well input from thermoreceptors, mechanoreceptors, and nociceptors.

4

Sense of Smell

Olfaction, the sense of smell—like the sense of taste—originates with chemoreceptors that respond to chemicals in solution. Although modest compared to the noses of many other animals, the human nose can discriminate among thousands of different odor substances; most people can tell the difference between 2,000 to 4,000 odors, and some can detect up to 10,000 odors. For instance, if you were blindfolded, you could likely tell the difference between your best friend's house and other homes simply by the odors. Some individuals, such as professional wine tasters and tea tasters, make a living through the use of their sense of smell.

Olfaction is important because it provides information about the quality of the air we breathe. For example, smelling a noxious gas, such as ammonia, will cause a reflex that interrupts our breathing. In addition, we may receive subtle cues about another person's mood by the odors he or she gives off. In fact, perfume manufacturers take advantage of some of these odors. Interestingly, on average, women tend to be more sensitive to odors than men are, and they are more sensitive to certain odors near the time of ovulation compared with other phases of their menstrual cycle.

LOCATION OF OLFACTORY RECEPTORS

The **nasal cavity**, the space between the roof of the mouth and the floor of the skull, is divided into two spaces, left and right, by a partition called the **nasal septum**. The surface area of each space is enlarged by folds that form ridges called **conchae**. The adult human has three conchae, arranged one on top of the other on each side of

the nasal septum. The entire nasal cavity is lined with a mucous membrane that includes epithelial cells with many hair-like structures (cilia) and goblet cells (which produce mucus). However, the nasal receptor cells, called **olfactory cells**, are

DID YOU KNOW?

Pheromones are chemicals, somewhat similar to hormones, but instead of being transported by the bloodstream, they move through the air from one person to another, thereby allowing one individual to influence the physiology of another. For example, pheromones in a person's bodily secretions may affect the sexual physiology of others. A woman's sweat appears to influence the timing of other women's menstrual cycles. This may explain the so-called "dormitory effect," in which women who live together tend to get their menstrual periods around the same time. In addition, the presence of women makes a man's beard grow faster, and the presence of men seems to influence the timing of female ovulation. When a woman is ovulating or close to ovulation, her vaginal secretions contain pheromones that have been shown to raise men's testosterone levels.

An interesting study was conducted to find out whether a woman's choice of a mate might be influenced by smell. A group of men was asked to wear the same T-shirt for several days in a row. The shirts were then laid out, one next to the other. Without knowing who had worn which shirt, women were asked to tell which shirts smelled pleasant or unpleasant. Interestingly, the shirts that the women said had a pleasing odor had been worn by men who had an HLA (human leukocyte antigen) complex that was different from that of the woman who smelled them. In contrast, the shirts each woman found unpleasant to smell had been worn by men with an HLA complex similar to her own. It turns out that mates who have different HLA complexes may increase the chances that their offspring will have a stronger immune system. Thus, from an evolutionary point of view, there might be an overall survival advantage for women to be influenced by odor when selecting their mates.

found only in a small area called the **olfactory region**, which is a yellow-tinged patch about 5 square centimeters (0.8 sq in). It contains 10 to 20 million cells. The olfactory region is located over all of the upper concha and as islands on the middle concha. The olfactory region also contains supporting cells and basal cells, similar to those found in taste buds. However, unlike taste cells, which are epithelial cells, olfactory cells are actual neurons, or nerve cells.

The olfactory epithelium is not in the best position for detecting odors because the air that enters the nasal cavity has to make a hairpin turn to stimulate the receptors before going into the respiratory passage below. In fact, a normal, relaxed inhalation carries about 2% of the air breathed in to the olfactory regions. However, sniffing, which draws air upward across the olfactory epithelium, increases the sense of smell.

In the human fetus, the mucous membrane on the septum contains closed tubules that appear to lead to nowhere. These structures form what is left of the vomeronasal organ, which is an olfactory organ that plays an important role in many amphibians, reptiles, and mammals other than humans. For instance, when a snake sticks out its forked tongue, it is picking up chemicals in the air, which it then touches to its vomeronasal organ. The function of the vomeronasal organ in humans is debated.

STRUCTURE OF THE OLFACTORY REGION

The **olfactory epithelium** contains olfactory cells, basal cells, and supporting cells (Figure 4.1). The supporting cells contain a yellow-brown pigment, which gives the olfactory epithelium a yellowish hue. As with taste buds, the basal cells replace other cell types in the olfactory epithelium as they die off. The olfactory cells, which are shaped like bowling pins, are rather unique. They are the only neurons in the body that are directly exposed to the external environment. They are also one of the few types of neurons that are continuously replaced throughout life. In fact, their typical life span is about 60 days,

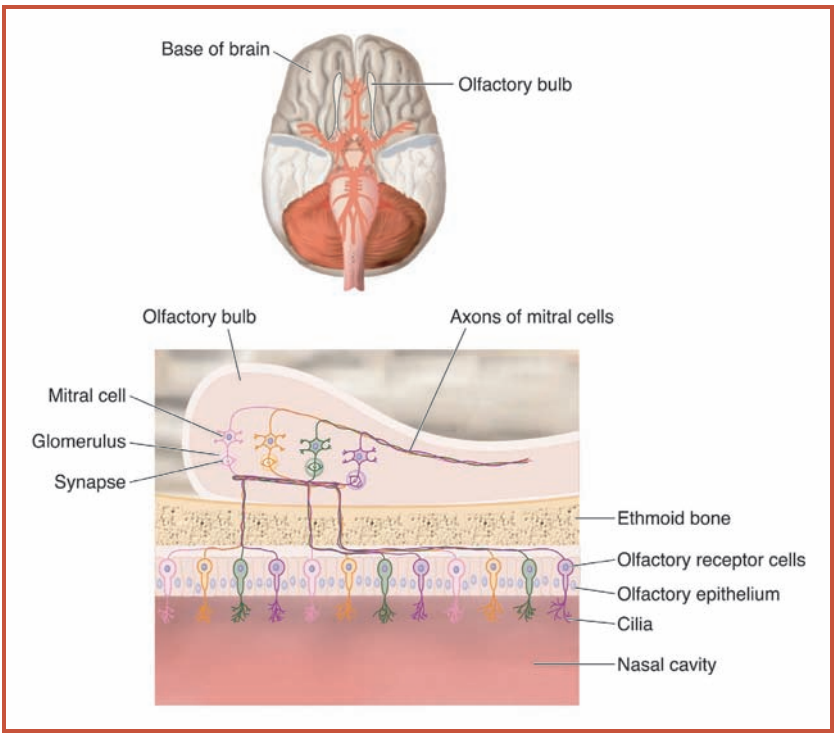

Figure 4.1 **The olfactory epithelium is located on the roof of the nasal cavity. When you inhale an odor, it dissolves in the fluid on the olfactory epithelium and binds to receptors on the cilia of the olfactory receptor cells. This diagram shows the structure of the olfactory bulb and the olfactory epithelium.**

after which they are replaced by the continuous division and differentiation of basal cells.

The olfactory cells have 10 to 20 long, hair-like structures called cilia at their apical (outward-facing) poles. These **olfactory cilia** give the olfactory epithelium more surface area with which to detect smells. Amazingly, the exposed surface area generated by olfactory cilia actually approaches that of the entire body surface area, about 2 square meters (3,100 sq in)!

The olfactory cilia are typically covered by a coat of mucus, which dissolves substances in the air that cause

odors. The molecules of an odor must go through part of this mucus layer before they get to the olfactory cilia. The mucus is produced by supporting cells of the olfactory epithelium and by **olfactory glands** in the connective tissue underneath. The basal end of each olfactory cell tapers to become an **axon** (the long, narrow part of a nerve cell that sends electrical signals called **action potentials**). These axons leave the nasal cavity through pores in part of the bone of the skull. Together, these axons are called the **olfactory nerve**.

ODOR SENSATIONS

Although the basic tastes have been divided into five types, efforts to identify primary odors have been inconclusive and remain controversial. For practical purposes, we can describe a series of qualities or odor classes. A few of these primary odors (and the chemicals that produce them) include flowery (β-phenylethyl alcohol), etheric (benzylacetate), musky (ring ketones), camphorous (camphor), sweaty (butyric acid), rotten (hydrogen sulfide), and pungent (formic acid). It should be

DID YOU KNOW?

Motile cilia (those that are capable of movement) in the part of the nasal cavity that handles breathing control the flow of mucus that is produced by supporting cells and olfactory glands. Cilia are sensitive to temperature. When it gets cold, they become temporarily paralyzed. This explains why your nose "runs" when you inhale outside air on a cold winter's day—the mucus is still being produced, but the cilia cannot move it toward your pharynx. This is also why your nose stops running soon after you go indoors. The cilia of the respiratory tract are also paralyzed by cigarette smoke, which is why many smokers may develop a chronic cough. The cough is the body's way of trying to clear mucus that gets trapped in the respiratory tree.

noted, however, that substances that are similar chemically may fall into different odor classes, while members of a single odor class can have very different chemical structures.

Some studies suggest that there are at least 1,000 "odor genes." Each gene apparently codes for a unique odor receptor molecule. However, given the large number of odors we can detect, it is unlikely that an olfactory cell has a specific receptor molecule for each and every odor substance. Instead, it seems more likely that each receptor molecule responds to a number of different odors, and each odor substance may bind to several different receptors. Evidence that receptor molecules interact with more than one odor substance can be seen in the phenomenon of partial **anosmia**, a condition in which a person cannot smell a specific odor or odors. It turns out that about 0.5% of the people in Europe have symptoms of partial anosmia. When these people try to smell different odors, they cannot detect a small number of substances that smell similar (e.g., certain musky odors). Thus, the existence of partial anosmia indicates that the number of odor qualities we can detect is limited to some extent and that receptor molecules can be stimulated by more than one odor substance.

Another problem with defining odor qualities is that it is hard to determine what properties are needed to give a substance an odor. For instance, in order for us to smell something, it must be volatile (able to evaporate and exist as a gas) and be carried by inhaled air into the nasal cavity. In addition, the substance must dissolve in the fluid that coats the olfactory epithelium. However, the intensity of smells is not just related to its volatility. For instance, water is highly volatile (evaporates easily), but has virtually no odor. In contrast, musk, found in animal scent glands, has a very distinctive odor, but is not very volatile. In general, odorants are small organic molecules, and the strongest smells usually go along with molecules that are very soluble in both water and lipids. One example is butyl mercaptan, which has a very low detection

threshold. This chemical gives off an unpleasant, rotten, garlicky smell, which is why it is often added to natural gas to make gas leaks easier to detect.

TRANSDUCTION DURING SMELL

Dissolved chemicals (odorants) stimulate olfactory receptors by binding to a receptor protein or proteins in the cilia of olfactory cells. This, in turn, activates **adenylate cyclase**, an enzyme that turns adenosine triphosphate (ATP) into **cyclic adenosine monophospate** (**AMP**), or cAMP. The cAMP molecules send signals between cells and interact with sodium channels in the olfactory cell membrane, causing them to open. Open sodium channels allow positively charged sodium ions (Na^+) to flow inward, which depolarizes the cell membrane. That is, it gives the inside of the cell a less negative charge compared to the outside of the cell. A large enough depolarization triggers an action potential in the nerve axon, which goes to the end of the olfactory tract, the **olfactory bulb** of the brain. Some odors stimulate nociceptors rather than olfactory cells. These include ammonia, menthol, chlorine, and hot peppers. One example is the "smelling salts" used to help revive an unconscious person. These substances strongly stimulate nociceptors with ammonia fumes.

DID YOU KNOW?

Although olfactory receptors are constantly replaced, the total number of receptors we have declines as we age, and our remaining receptors become less sensitive. As a result, older people often have difficulty detecting odors in low concentrations. This decrease in the number of receptors and their sensitivity helps explain why your grandmother may apply too much perfume or your grandfather may overdo his application of aftershave.

THE OLFACTORY PATHWAY

Olfactory nerve fibers pass through part of the skull and enter a pair of olfactory bulbs beneath the frontal lobes of the brain. There, the nerves connect with neurons called **mitral cells** and form complex structures called **glomeruli** (singular is *glomerulus*). Each glomerulus receives only one type of odor signal, and different odors, which would excite a variety of receptor types, likely activate different glomeruli. The mitral cells serve to refine and amplify signals that come from olfactory nerves and then send those signals to other areas of the brain via **olfactory tracts** (the axons of mitral cells). Although as few as four molecules of an odorous substance can activate an olfactory receptor and its associated nerve fibers, we may not necessarily be aware of the stimulus. This is because olfactory bulbs also house **granule cells**, which can inhibit the activity of mitral cells. When this happens, only highly excitatory olfactory impulses are transmitted from the glomeruli. This inhibition helps cause olfactory adaptation, a decrease in responsiveness during continued stimulation, and explains why we may become unaware of our own body odor or a gas leak in a kitchen. In fact, olfactory receptors adapt very little to a persistent stimulus, and it is instead adaptation in the central nervous system that makes us quickly lose awareness of a particular smell, but remain sensitive to others.

When mitral cells are activated, nerve impulses flow from the olfactory bulbs to two main destinations via the olfactory tracts. Some signals go through a sorting center in the brain, called the **thalamus**, to the cerebral cortex, where smells are consciously interpreted and identified. Olfactory signals also are sent to other regions of the brain, which include the **amygdala** and **hypothalamus**, and other parts of the **limbic system** (Figure 4.2). The limbic system plays an important role in feeling emotions, and the hypothalamus contains centers that control the autonomic (unconscious) functions of our body. Thus,

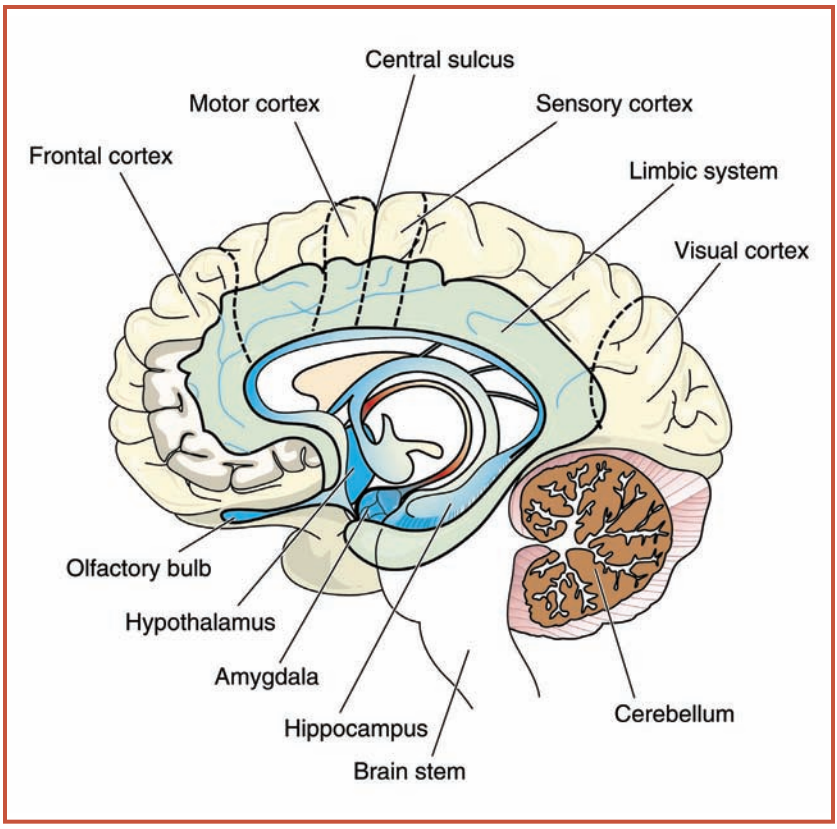

Figure 4.2 **This view of the human brain shows the structures that make up the limbic system, a portion of the brain that is important for feeling and interpreting emotions. The amygdala recognizes angry or fearful facial expressions, assesses danger, and elicits an appropriate response. Interestingly, smell signals go to the limbic system, where the odors may cause specific emotional responses and memories.**

signals generated by smell can trigger strong emotional and physical reactions by influencing the limbic system, even if we are not consciously aware of an odor. For example, the smell of certain foods can increase salivation and stimulate the digestive tract. The perfume industry expends considerable effort trying to develop odors that trigger sexual responses. In

contrast, odors associated with unpleasant items, such as raw sewage, a skunk, or decaying flesh can trigger a **fight-or-flight response**, and can even make us vomit. In addition, the cerebral cortex sends its own signals to the olfactory bulbs. These brain-generated signals can change the quality and significance of odors under different conditions. For instance, food may smell more appealing when you are hungry and may seem less appetizing after a large meal.

CONNECTIONS

The sense of smell (olfaction) is regulated by chemoreceptors, and we are capable of detecting thousands of different odor substances. The nasal cavity is divided into two spaces by a partition called the nasal septum. The surface area of each space is enlarged by folds that form ridges called conchae. Adult humans have three conchae. The entire nasal cavity is lined with a mucous membrane that includes ciliated epithelial cells and goblet cells (which produce mucus). Olfactory cells exist only in a small area called the olfactory region. This area also contains supporting cells and basal cells, which are similar to taste buds. However, unlike taste cells, which are epithelial, olfactory cells are neurons.

Olfactory cells undergo regular turnover throughout the life of an adult and have a life span of about 60 days, after which they are replaced by the continuous division and differentiation of basal cells. Olfactory cells have 10 to 20 long cilia at their apical poles. These olfactory cilia increase the amount of surface area available to receive odors. The olfactory cilia are typically covered by a coat of mucus, which helps dissolve airborne substances. The basal end of each olfactory cell tapers to become an axon, which leaves the nasal cavity through pores in the skull.

Efforts to identify primary odors have been inconclusive and controversial. Some studies suggest that there are at least 1,000 “odor genes.” In general, odorants (dissolved chemicals)

are small organic molecules, and the strongest smells are often associated with molecules that are easily dissolved in both water and lipids.

Smells stimulate olfactory receptors by binding to a receptor protein in the cilia of olfactory cells. This, in turn, activates adenylate cyclase, an enzyme that converts ATP to cyclic AMP (cAMP). The cAMP molecules stimulate sodium channels, which depolarize the membrane. A large enough depolarization fires an action potential in the nerve axon, which will be sent to the olfactory bulb of the brain. Some odors activate nociceptors rather than olfactory cells.

Olfactory nerve fibers pass through pores in the skull and enter a pair of olfactory bulbs. There, the nerves connect with mitral cells and form complex structures called glomeruli. The mitral cells refine and amplify smell signals, and then relay them to other areas of the brain. Granule cells inhibit the activity of mitral cells, so only highly excitatory olfactory impulses are transmitted from the glomeruli. This inhibition contributes to the mechanisms of olfactory adaptation. When mitral cells are activated, nerve impulses flow from the olfactory bulbs to the cerebral cortex, where smells are consciously interpreted and identified. Olfactory signals also are sent to the amygdala, hypothalamus, and other parts of the limbic system. These signals can trigger strong emotional and physical reactions.

5

Accessory Structures of the Eye

The adult eye (Figure 5.1) is a sphere with a diameter of about 2.5 cm (1 in). Only the front one-sixth of its surface is visible. The rest is enclosed and protected by a cushion of fat and walls of the **orbit** (the cavity in the frontal bone of the skull). The eye is a complex structure, and only a small part of its tissues are directly involved with **photoreception**, the conversion of light energy into chemical energy. Photoreception can lead to **vision**, the perception of objects in the environment by means of the light they emit or reflect. In fact, vision is a dominant sense for human beings; we rely on vision more than any other special sense. This is indicated by the fact that 70% of all the sensory receptors in our body are found in the eyes, and almost half of the cerebral cortex is involved with some aspect of processing vision.

The accessory structures of the eye include the eyebrows, eyelids, conjunctiva (outer surface of the eyeball), lacrimal apparatus (the structures that produce and secrete tears), and the extrinsic eye muscles.

EYEBROWS

The **eyebrows** are made up of short, coarse hairs that lie on the exterior ridges of the skull above the eye. Although they are

Figure 5.1 **Although the human eye is about 2.5 cm (1 in) in diameter, we can only see about one-sixth of its surface under normal conditions. This photograph is an excellent side view of the complete human eye.**

not directly involved with the visual process, they do serve important functions that help with vision. For instance, they can protect the eyes against glare, shade the eyes from sunlight, and prevent perspiration from running down the forehead into the eyes. They also have functions that are not related to vision; they can be used, for example, to enhance facial expressions, which is important in nonverbal communication. The eyebrows have special muscles that let them move both up and down and from side to side.

EYELIDS

The **eyelid** is a thin, movable fold of skin over each eye. It protects our eyes by preventing foreign objects and excessively bright light from reaching the eyeballs. It also keeps visual stimuli from disturbing us while we sleep. In addition, the eyelids act like miniature windshield wipers, sweeping foreign material

from the eye surface. Blinking (which takes place about every 3 to 7 seconds) keeps the surface of the eye free from dust and other debris, while also keeping the eye surface moist and lubricated with secretions (such as oil, mucus, and saline solution).

The free margins of the upper and lower eyelids are separated by the **palpebral fissure** and meet at the corners, which are called the **medial** and **lateral commissures**. In most Asian people, a vertical fold of skin called the epicanthal fold commonly appears on both sides of the nose and sometimes covers the medial commissures. The eyelid itself is composed largely of muscles—called the orbicularis oculi and levator palpebrae superious—that are covered with skin. When

DID YOU KNOW?

Light is a form of electromagnetic energy that travels through space as waves. Vision is well adapted for wavelengths of light within what we call the visible spectrum (400 to 700 nanometers [nm]) but not beyond. Why is this? In part, it is because most solar radiation that reaches the surface of the Earth falls within this range. Radiation of shorter wavelengths, such as ultraviolet (UV) light, is absorbed by the atmosphere's ozone layer. Radiation of longer wavelengths is filtered out of the atmosphere by carbon dioxide and water vapor. However, there also is a physiological explanation. To stimulate a receptor, light must produce a photochemical reaction in which the chemical structure of a molecule changes through its interaction with light energy. Radiation above 750 nm does not have enough energy to activate the visual process; it may feel warm (like the infrared radiation of a heat lamp), but it usually does not cause a chemical reaction. In contrast, radiation below 400 nm has so much energy that it kills cells. This is why ultraviolet radiation can be useful for sterilizing instruments, but has too much energy for the biochemical process of vision. Interestingly, some animals can detect radiation slightly beyond the range visible to humans. For instance, certain insects can see objects illuminated in the ultraviolet range that are invisible to mammals.

the orbicularis oculi contracts, the eye closes. The upper eyelid raises when the levator muscle contracts. The eyelid also has a supportive, fibrous, thick connective tissue sheet along the margin of the eyelid, called the **tarsal plate**. This structure holds the eyelid muscles in place.

Eyelashes are sturdy hairs coming out of the margins of the eyelids that help keep foreign matter and insects from reaching the surface of the eye. Touching the eyelashes stimulates hair receptors and causes us to blink.

The eyelids have several types of glands. The medial commissure contains the **lacrimal caruncle**, a soft tissue mass that contains sebaceous (secreting a fatty lubricant) and sweat glands. Its thick, whitish, oily secretion sometimes collects at the medial commissure, especially while we sleep. (It is often called the "sandman's eye-sand.") Along the inner margin of the eyelids are 20 to 25 modified sebaceous glands called **Meibomian glands**. These glands have ducts that open at the eyelid edge just behind the eyelashes. They secrete a lipid-rich product that moistens the eyelids and helps keep them from sticking together. This secretion also keeps tears from evaporating off the surface of the eye. Associated with the eyelash follicles are a number of smaller, more typical sebaceous glands, called the **glands of Zeis**. In addition, modified sweat glands known as ciliary glands lie between the eyelash hair follicles. Unfortunately, the glands of the eye can suffer from occasional infection by bacteria, which can form a **sty**—a painful, localized swelling something like a pimple on the eyelid.

CONJUNCTIVA

The **conjunctiva** (literally meaning "joined together") is an epithelium that covers the inner surfaces of the eyelids (palpebral conjunctiva) and the outer surface of the eye (ocular conjunctiva), excluding the cornea (the clear tissue over the pupil and iris). It is a mucous membrane covered by a special tissue called stratified squamous epithelium.

Its main function is to secrete a thin film of mucus that prevents the eyeball from drying out. The conjunctiva is highly sensitive to touch because it is filled with nerves. It also has many blood vessels. When these blood vessels are dilated, the eyes look "bloodshot." Damage or irritation to the conjunctiva can cause **conjunctivitis** (also called "pinkeye"). The most obvious symptom of conjunctivitis is reddening, due to dilation of the blood vessels beneath the epithelium. Conjunctivitis may be caused by infection with bacteria or viruses, and it is highly contagious. It also may result from physical or chemical irritation of the surface of the conjunctiva.

LACRIMAL APPARATUS

A constant flow of tears keeps the conjunctival surfaces moist and clean. The **lacrimal apparatus** is made up of several structures that produce, distribute, and remove tears. It includes the lacrimal gland with its associated ducts, lacrimal canals, a lacrimal sac, and a nasolacrimal duct (Figure 5.2).

The **lacrimal gland** is about the size and shape of an almond, and is nestled in a shallow fossa (depression) of the frontal bone of the skull, above the lateral end of the eye (the side farthest from the nose). It is visible through the conjunctiva when the eyelid is turned inside out. The lacrimal gland releases

DID YOU KNOW?

Because tears eventually drain into the nasal cavity, an abundance of tears from crying or watery eyes (like you may get with allergies) can result in a runny nose. Once the tears enter the nasal cavity, they normally flow back into the throat (through the action of cilia) and we swallow them. However, when we have a cold or allergy, the nasolacrimal ducts can become swollen and obstructed, which prevents tears from draining properly. This, in turn, makes tears overflow from the brim of the eye.

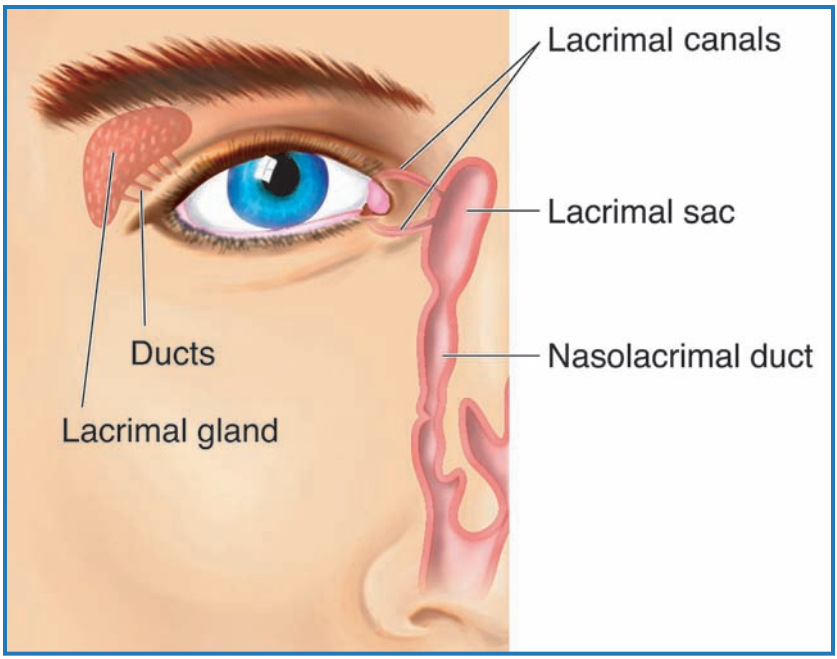

Figure 5.2 **The lacrimal apparatus includes the lacrimal gland and the ducts that drain lacrimal secretions (tears) into the nasal cavity. Lacrimal fluid includes mucus, antibodies, and lysozyme, an enzyme (protein) that kills bacteria. These ingredients allow tears to moisten, cleanse, and protect the surface of the eye.**

about 1 milliliter per day of a dilute saline (salt) solution called **lacrimal secretion**, commonly known as tears. Tears drain to the surface of the conjunctiva through 12 or so short ducts. Lacrimal secretion contains water, salts, mucus, antibodies, and **lysozyme**, an enzyme (protein) that has antibacterial properties. Thus, tears reduce friction, remove debris, help prevent bacterial infection, and bring nutrients and oxygen to the conjunctiva.

Once the lacrimal secretions have reached the eye surface, they mix with the products of accessory glands, such as the oily secretion of the Meibomian glands. Blinking sweeps tears across the eye surface, and they accumulate at the medial commissure, where they enter the **lacrimal canals** through

two tiny openings called **lacrimal puncta** (these are visible as two tiny dots on the medial margin of each eyelid). From the lacrimal canals, the tears drain into the **lacrimal sac**, and then into the **nasolacrimal duct**, which delivers tears to the **inferior meatus** of the nasal cavity.

EXTRINSIC EYE MUSCLES

Six strap-like **extrinsic eye muscles** control the movement of each eyeball. The six muscles attach directly to the external surface of the eyeball and to the walls of the orbit. These muscles allow the eyes to follow a moving object and also help maintain the shape of the eyeball, as well as hold the eye within the orbit. The outer eye muscles are among the most precisely and rapidly controlled skeletal muscles in the body. This is because they have a high ratio of nerves to muscle fibers.

YOUR HEALTH: Eyes Out of Alignment

Unfortunately, a person cannot properly focus images from each eye if the movements of the external muscles of the two eyes are not perfectly coordinated. In such cases, a person will usually see two images instead of one, a condition known as diplopia (double vision). This can result from paralysis or weakness of certain outer muscles or it may occur temporarily when someone drinks large amounts of alcohol. In addition, a congenital (inherited) weakness of the external eye muscles may cause strabismus, an abnormal alignment of the eye that is sometimes called "wandering eye." In some instances, only the eye that the person can control is used for vision. When this is the case, the brain ignores input from the wandering eye, which can become functionally blind. Less severe cases of strabismus can be treated with eye exercises to strengthen weak muscles or by placing a patch over the stronger eye, which forces the person to use the weaker eye. In more serious cases, however, surgery may be needed to repair the eye muscle.

The outer eye muscles handle two basic types of eye movements: saccades and scanning. **Saccades** are small, jerky movements that quickly move the eye from one spot to another, allowing us to see an entire visual field in a short period of time. In contrast, **scanning movements** track an object that is moving; that is, they allow us to follow a particular object moving in our visual field or to maintain our gaze on a fixed object as we move our heads.

CONNECTIONS

The adult eye is a sphere that is enclosed and protected by a cushion of fat and the walls of the orbit. Photoreception can lead to vision, the perception of objects in the environment by means of the light they emit or reflect. Eyebrows are short, coarse hairs that lie on the outside ridges of the skull above the eye. They protect the eyes against glare, shade our eyes from sunlight, and keep perspiration from running down the forehead into the eyes.

The eyelids protect our eyes by blocking foreign objects and light that is too bright. Blinking (which happens about every 3 to 7 seconds) keeps the surface of the eye free from dust and other debris, and also keeps the eye surface moist and lubricated with secretions (like oil, mucus, and saline solution).

The free margins of the upper and lower eyelids are separated by the palpebral fissure, and meet at the corners, which are called the medial and lateral commissures. The eyelid also contains a sheet of supportive, fibrous, thick connective tissue along its margin, called the tarsal plate.

Several types of glands are associated with the eyelids. The medial commissure contains the lacrimal caruncle, a soft mass of tissue that contains sebaceous and sweat glands. Its thick, whitish, oily secretion sometimes collects at the medial commissure, especially when we sleep. Along the inner margin of the eyelids are modified sebaceous glands called Meibomian

glands whose lipid-rich secretion lubricates the eyelids and helps keep them from sticking together.

The conjunctiva is an epithelium covering the inner surfaces of the eyelids and the outer surface of the eye. Its main function is to produce a thin mucus film that prevents the eyeball from drying out. The conjunctiva is highly sensitive to touch because it is richly packed with nerves. It is also supplied with many blood vessels. Damage, irritation, and infection to the conjunctiva can cause conjunctivitis.

A constant flow of tears keeps the conjunctival surfaces moist and clean. Lacrimal fluid contains water, salts, mucus, antibodies, and the enzyme lysozyme. Thus, tears reduce friction, remove debris, inhibit bacterial infection, and help bring nutrients and oxygen to the conjunctiva. The lacrimal apparatus consists of the lacrimal gland with its associated ducts, lacrimal canals, a lacrimal sac, and a nasolacrimal duct. The lacrimal gland continually releases a dilute saline solution called lacrimal secretion (tears). Blinking sweeps tears across the eye surface, and they accumulate at the medial commissure, where they enter the paired lacrimal canals via two tiny openings called lacrimal puncta. From the lacrimal canals, the tears drain into the lacrimal sac, and then into the nasolacrimal duct, which delivers tears to the nasal cavity.

The movement of each eyeball is controlled by six strap-like outer eye muscles that attach directly to the external surface of the eyeball and to the walls of the orbit. These muscles allow the eyes to follow a moving object and also help maintain the shape of the eyeball, as well as hold it in place. The external eye muscles are responsible for two basic types of eye movements: saccades and scanning.

6

Structure of the Eye

Each eye is a slightly irregular hollow sphere, a little smaller than a Ping-Pong ball. The wall of the eye contains three distinct layers, called tunics, and two cavities (Figure 6.1).

THE TUNICS

The outermost layer is called the **tunica fibrosa**. It is divided into two regions: the sclera and cornea. The tendon-like **sclera**, which is the white part of the eye, consists of dense, fibrous connective tissue perforated by blood vessels and nerves. It protects and shapes the eyeball, and provides a sturdy site for the outer eye muscles to anchor. At the rear, the sclera connects with the dura mater—a membrane that covers the brain.

In contrast to the sclera, the **cornea** forms a transparent region that admits light into the eye. This is accomplished by a highly organized arrangement of collagen (a type of protein) fibers that minimizes the scattering of light. Because it is important for the cornea to be transparent, it contains no blood vessels (its superficial epithelial cells get oxygen and nutrients from the tears that flow across its surface). There are numerous nerve endings in the cornea; in fact, it is the most sensitive portion of the eye. The cornea is also part of the light-bending apparatus of the eye. Most of the bending of light needed to focus an image on the retina actually occurs through the cornea.

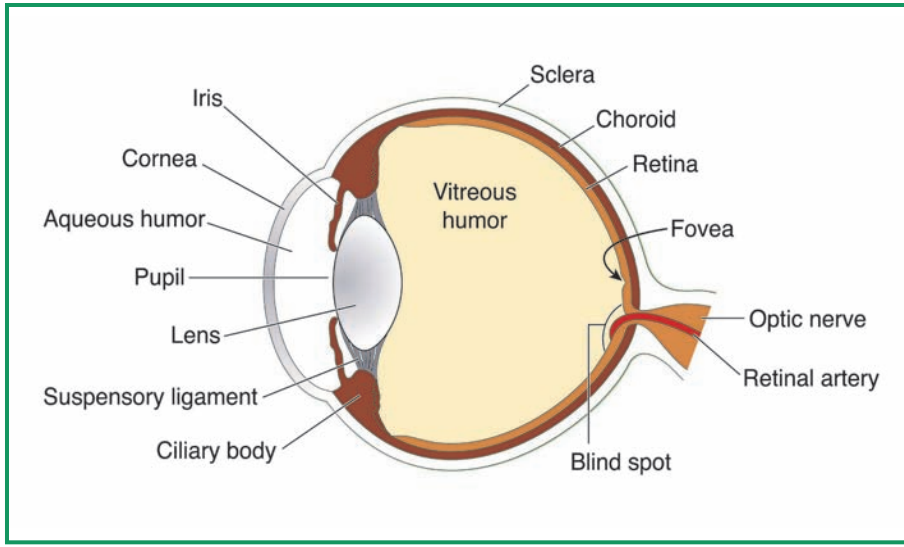

Figure 6.1 **The cornea and lens focus light rays onto the fovea, the part of the retina that has the most cones. When light is focused directly on the optic nerve (called the blind spot), the person cannot see the light. Because our two eyes have overlapping fields of view, and because our brains are able to "fill in" missing details, we don't see any interruptions or gaps in the images around us.**

The middle layer of the eye is called the **tunica vasculosa**, or *uvea* (which means "grape," since it resembles a peeled grape when it is dissected). It consists of three regions: the choroid, ciliary body, and iris. The **choroid** is a deeply pigmented membrane with many blood vessels. Its deep brown pigment (melanin) is produced by specialized cells called melanocytes and helps absorb light, preventing it from scattering and reflecting inside the eye. At the front of the eye, the choroid becomes the **ciliary body**. The ciliary body is made of interlacing bundles of smooth muscle, which are important for controlling the shape of the lens. The rear surface has radiating folds that contain capillaries (tiny blood vessels), which secrete the **aqueous humor**, a fluid that fills the anterior (front) chamber. The **iris**, the visible colored part of the eye, is an adjustable partition made of muscle and connective tissue that controls the diameter of the **pupil**, its central opening. The iris has two

layers of smooth muscle that allow it to make the pupil narrow or widen. In close vision or in bright light, the pupil gets smaller. In contrast, the pupil dilates (widens) for distant vision or in dim light, allowing more light to enter the eye. The constriction of the pupil in response to light is called the **pupillary reflex**. Interestingly, both pupils constrict even if light hits only one eye.

The **sensory tunic** is the innermost layer of the eye. It consists of an outer single-cell-thick **pigmented layer** and a thicker, transparent inner layer called the **retina**. The pigmented epithelial cells in the outer layer, like those of the choroid, absorb light so that it does not scatter in the eye. This pigmented layer stores vitamin A, which is needed by the retina's photoreceptor cells. The retina also contains supporting cells and neurons that perform preliminary processing and integration of visual information. Some of these include **bipolar cells** and **ganglion cells**, where action potentials are generated (Figure 6.2). The **optic nerve**, which carries impulses for the sense of sight, exits the eye at the **optic disk** in the retina. This region is

YOUR HEALTH: Corneal Injuries

Damage to the cornea can cause blindness even if the rest of the eye is perfectly normal. Although the cornea has some ability to repair itself, corneal injuries from severe scratches or other accidents must be treated quickly to prevent severe vision loss. Restoring vision after corneal scarring generally requires the replacement of the cornea through a transplant. In fact, corneal replacement is probably the most common form of transplant surgery. Because there are no blood vessels in the cornea to carry white blood cells, which attack foreign tissues, corneal transplants can be performed between unrelated individuals. Corneal grafts are taken from the eyes of donors who have recently died from illness or in accidents. The tissue should be removed within 5 hours of the donor's death for the best results.

also called the **blind spot**, because it has no photoreceptors. Thus, light focused on it cannot be seen. Finally, the retina contains blood vessels that supply tissues lining the rear cavity. The central retinal artery and vein pass through the center of the optic nerve and emerge on the surface of the optic disk.

PHOTORECEPTORS

There are two types of photoreceptors in the neural retina: rods and cones. The most numerous are the **rods**, which are used for vision in dim light and for peripheral vision (seeing from the sides of the eye). Rods do not discriminate between different colors of light, nor do they provide sharp images. That is why colors are indistinct and the edges of objects fuzzy when we see them in dim light or at the edges of our visual field. In contrast, **cones** work in bright light and give us clear and sharp color vision.

Rods and cones are not evenly distributed across the surface of the retina. Approximately 125 million rods form a broad band around the edge of the retina. Roughly 6 million

DID YOU KNOW?

The *iris* (from the Greek word for "rainbow") contains chromatophores (cells bearing pigment) that produce the pigment melanin. Although irises come in different colors, they only contain brown pigment. Why, then, are people's eyes different colors? It has to do with the amount—not the type—of pigment produced. High concentrations of melanin give the iris a black or brown color. However, if the amount of pigment produced is small and is only found on the rear surface, the shorter wavelengths of light can be scattered from the unpigmented cells, making the iris look blue or green. This process is similar to the scattering of shorter wavelengths of light in the atmosphere, which gives the sky its blue color. The quality of light that strikes the eye can also subtly change the hue of the iris.

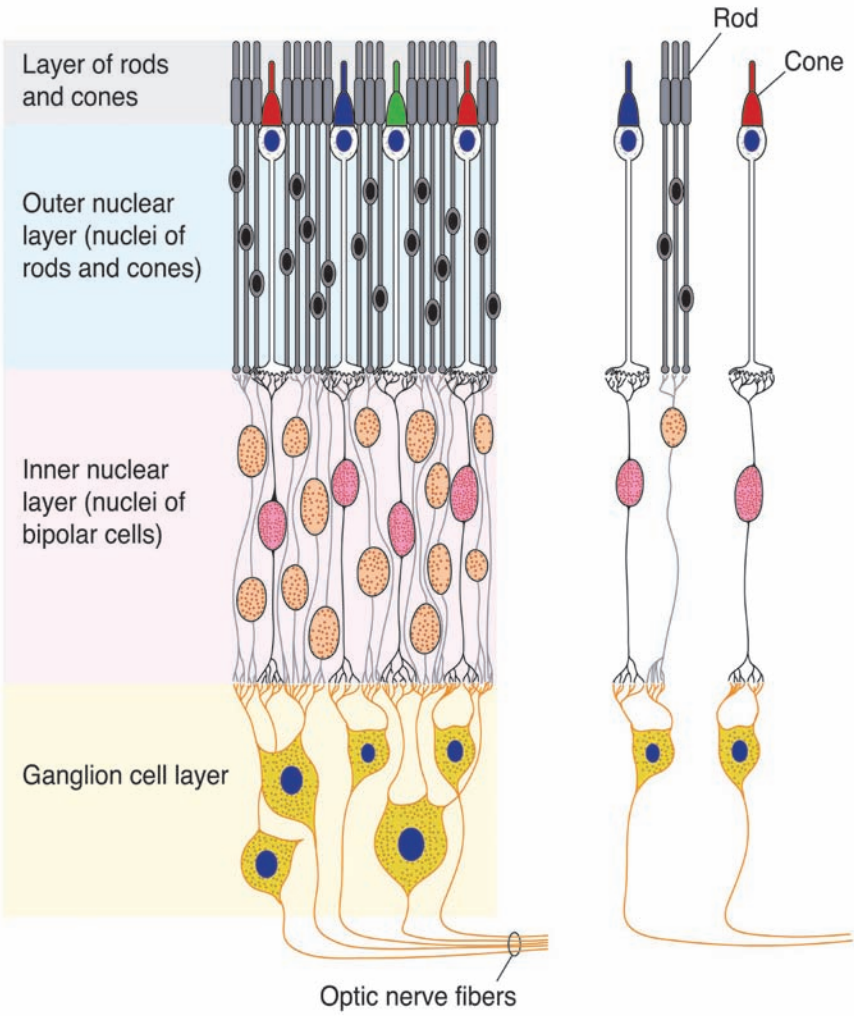
Rod
Cone
Layer of rods and cones
Outer nuclear layer (nuclei of rods and cones)
Inner nuclear layer (nuclei of bipolar cells)
Ganglion cell layer
Optic nerve fibers

Figure 6.2 The retina has three major kinds of neurons: photoreceptors (rods and cones), bipolar cells, and ganglion cells. Bipolar and ganglion cells fire action potentials that send the brain visual signals, while the rods and cones help us to see in dim light and in color, respectively.

cones span the rear surface of the retina surface. The **macula lutea** ("yellow spot") is a retinal region about 3 mm (0.12 in) in diameter that contains mostly cones. Its central portion, the **fovea centralis**, has no rods and contains the highest concentration of cones. The fovea (plural is *foveae*) is where light is focused when we look directly at an object to give us the sharpest image. Each fovea is about the size of the head of a pin (0.4 mm; 0.02 in). As a result, for us to visually comprehend a scene that is rapidly changing, our eyes must flick rapidly back and forth to give the foveae images of different parts of the visual field.

CAVITIES OF THE EYE

The ciliary body and lens divide the interior of the eye into a large **posterior** (rear) **cavity**, which contains a clear, gelatinous

YOUR HEALTH: Retinal Detachment

Although the two layers of the sensory tunic are close together, they are not fused. This makes the eye vulnerable to retinal detachment, a condition in which the retina separates from the pigmented layer, allowing the jelly-like vitreous humor to seep between them. Retinal detachment can result from a sudden impact to the eye or when the head stops moving suddenly and is then jerked in the opposite direction (as can occur in a car accident or when bungee jumping). Some people describe the experience as a curtain being drawn across their eye. Others say they see soot-like spots or flashes of light. Retinal detachment deprives the retina of its nutrient source. Consequently, unless the two layers of the sensory tunic are reattached quickly, photoreceptors will degenerate and the person will become blind. The reattachment is generally performed by fusing the two layers together using a laser beam focused through the cornea, or by attaching a scleral buckle, a band that holds the retina in place.

material called the **vitreous humor**. Vitreous humor binds a large amount of water, allowing it to transmit light, hold the retina against the pigmented layer, and put pressure on the inside of the eye (called intraocular pressure), thereby helping to counteract the pulling force of the outer eye muscles. The vitreous humor forms before birth and lasts for an entire lifetime.

The smaller **anterior** (front) **cavity** is subdivided into two chambers. The **anterior chamber** extends from the cornea to the iris, and the **posterior chamber** lies between the iris and the ciliary body and lens. Both chambers are filled with aqueous humor, a clear fluid secreted by the ciliary body that is similar in composition to blood plasma. Aqueous humor is produced and drained continually, and is in constant motion. It flows from the posterior chamber through the pupil into the anterior chamber, where it is drained into the blood of the veins via the **canal of Schlemm**. Normally, the rate of removal balances the rate of secretion, about 1–2 microliters/min (μl/min), resulting in a constant intraocular pressure of 12–21 mm Hg. This, in turn, helps support the eyeball internally, much like air inside a balloon. The aqueous humor also provides nutrients and oxygen to the lens and cornea, while carrying away their metabolic waste products.

DID YOU KNOW?

Cones cannot function in very dim light. For example, when you try to look at a dim star, you might be unable to see it when you look directly at it. However, the star often becomes more visible when you turn your head slightly and look a little to one side. This is because shifting your gaze moves the image of the star from the foveae of your eyes, where there is not enough light energy to stimulate cones, to the retinal periphery, where the light can stimulate rods, which have a relatively low threshold.

THE LENS

The **lens** is a biconcave, flexible structure that is suspended behind the pupil by a ring of fibers called the **suspensory ligament**, which attaches to the ciliary body. The main function of the lens is to focus visual images on the retinal photoreceptors. Like the cornea, it is avascular, meaning that it has no blood vessels (since blood vessels would prevent it from being transparent). The lens has two regions: the lens epithelium and the lens fibers. The lens epithelium is confined to the anterior surface. However, its cells differentiate into lens fibers that have no nuclei and few organelles (internal cell structures). These cells contain precisely folded transparent proteins. Because new lens fibers are always being added, the lens gets bigger as we age. Over time, the lens becomes less elastic, which gradually prevents it from being able to focus light. This condition, known as **presbyopia**, explains why people over the age of 40 commonly need reading glasses.

YOUR HEALTH: Retinopathy

The retina can be examined with an instrument called an ophthalmoscope, which both illuminates and magnifies an image. Eye examinations not only evaluate the eye's visual system, but also allow doctors to check blood vessels for signs of hypertension (high blood pressure), diabetes mellitus (a disorder that affects how the body uses glucose), and atherosclerosis (hardening of the arteries). Retinopathy is a disease of the retina. Diabetic retinopathy develops in many individuals with diabetes mellitus. Diabetes can cause serious circulatory problems, including the degeneration and rupture of retinal blood vessels. As a consequence, a loss of clarity of vision (visual acuity) can occur over time as photoreceptors degenerate from oxygen starvation.

CONNECTIONS

Each eye is a sphere composed of three distinct layers, called tunics, and two cavities. The outermost layer, called the tunica fibrosa, is divided into two regions: the sclera and cornea. The tendon-like sclera consists of dense connective tissue perforated by blood vessels and nerves. It protects and shapes the eyeball, and provides a sturdy anchoring site for the outer eye muscles. The cornea is modified to form a transparent region that admits light into the eye and is part of the light-bending apparatus of the eye.

The middle layer of the eye, called the tunica vasculosa, consists of three regions: the choroid, ciliary body, and iris. The

YOUR HEALTH: Glaucoma

If aqueous humor begins to drain more slowly but is still produced at the same rate, the pressure within the eye may reach dangerously high levels, a condition known as glaucoma. Since the fibrous tunic cannot expand significantly, the increasing pressure will squeeze the retina and optic nerve. If untreated, the person will eventually go blind. Glaucoma affects about 2% of the population over age 35, and, unfortunately, there are usually no symptoms until damage has already occurred. Late signs include seeing halos around light or flashes of light, and blurred vision.

Testing for glaucoma is a simple procedure. A puff of air is aimed at the sclera or the sclera is touched with a small probe, and then the amount of deformation that either causes is measured, giving a reading of the pressure inside the eye. Most eye-care specialists encourage people to have a glaucoma test done every year after the age of 40. People who have glaucoma usually give themselves eye drops that help drain the aqueous humor. A doctor may also perform corrective surgery, piercing the wall of the anterior chamber with a laser beam to increase drainage.

choroid is a highly vascular, deeply pigmented membrane. Its deep brown pigment (melanin) helps absorb light, preventing it from scattering and reflecting within the eye. At the front of the eye, the choroid becomes the ciliary body, which consists of interlacing smooth muscle bundles. These are important for controlling the lens shape. The posterior surface has radiating folds that contain capillaries, which secrete the aqueous humor. The iris, the visible colored part of the eye, controls the diameter of the pupil, its central opening. The iris has two layers of smooth muscle that allow it to adjust pupil size. The sensory tunic, the innermost layer of the eye, consists of an outer single-cell-thick pigmented layer and a thicker, transparent inner layer called the retina. Along with photoreceptors, the retina also contains supporting cells and neurons that

YOUR HEALTH: Cataracts

How transparent the lens is depends on a precise combination of structural and biochemical characteristics. The lens can lose its transparency when this balance is disturbed, forming a cataract. A cataract is a clouding of the lens that makes vision appear distorted, as if you were looking through frosted glass. Cataracts may result from drug reactions, injuries, or radiation. However, the most common causes are age-related hardening and thickening of the lens or as a secondary consequence of diabetes mellitus. Heavy smoking and frequent exposure to ultraviolet radiation (like that of intense sunlight) increase the risk of developing cataracts. Ultimately, cataracts happen when the deeper lens fibers don't get enough nutrients. This leads to changes that result in the clumping of proteins. If the lens becomes sufficiently opaque, the person will become functionally blind. However, this condition can be treated surgically by removing the lens and replacing it with an artificial one. Then vision can be fine-tuned with eyeglasses or a contact lens.

handle the early processing of visual information. The optic nerve leaves the eye at the optic disk in the retina, also called the blind spot.

There are two types of photoreceptors in the retina: rods and cones. The rods are used for vision in dim light and for peripheral vision, and cones operate in bright light and provide sharp color vision. The macula lutea is a retinal region that contains mostly cones. Its central portion, the fovea centralis, has no rods but contains the highest concentration of cones. The fovea is the place where light is focused when we look directly at an object to give us the sharpest image.

The ciliary body and lens divide the interior of the eye into a large posterior cavity, which contains a clear, gelatinous material called the vitreous humor. The smaller anterior cavity is subdivided into two chambers: anterior and posterior. Both chambers are filled with aqueous humor, a clear fluid that is secreted by the ciliary body and flows from the posterior chamber through the pupil into the anterior chamber, where it is drained into the blood of the veins via the canal of Schlemm.

The lens is a biconcave, flexible structure that is suspended behind the pupil by a ring of fibers called the suspensory ligament, which attaches to the ciliary body. The main function of the lens is to focus the visual image on the retinal photoreceptors. The lens fibers contain precisely folded transparent proteins. Because new lens fibers are continually added, the lens enlarges as we age and also becomes less elastic, which decreases the lens's ability to focus light.

7

Sense of Sight

Although photoreception depends on the stimulation of photoreceptors, the visual process also requires a mechanism for focusing light rays on the retina. In many respects, the image-focusing system of our eyes works on a principle similar to that of a camera. For instance, the eye has an adjustable iris, something like a camera's shutter, which can change the amount of light that enters the eye by altering the diameter of the pupil. Behind the pupil is a lens, a structure designed to focus light on the retina in a manner similar to a camera lens focusing light on film. Thus, the retina, a structure that contains photoreceptors, can be compared to the film in a camera.

PROPERTIES OF LIGHT

Our eyes respond to a specific region of the **electromagnetic spectrum** called **visible light**, which has a wavelength range of about 400 to 700 nm (1 nm = 10^{-9} m, or one-billionth of a meter). Although light travels in waves with wavelengths that can be measured, it is actually made up of small packets of energy called **photons**. When visible light passes through a prism, a **spectrum** (band of colors) can be seen. In fact, a rainbow is a spectrum formed when lots of tiny water droplets act together as prisms in the atmosphere during a rain shower.

REFRACTION

Light rays travel in straight lines at very fast speeds—300,000 km/sec (186,000 miles/sec) in a vacuum. Although the

speed of light is constant in a given medium, it changes when light passes through one transparent medium into another with a different density. For this reason, light slows down slightly in air, water, and glass. In addition, these changes cause a bending, or **refraction**, of light when it meets the surface of a different medium at an oblique angle. Refraction can easily be demonstrated by placing a straw in a partially filled glass of water. The straw will appear to "break" at the place where the air meets the water. The **refractive index** of a medium measures how much it retards (and therefore bends) light rays relative to air.

DID YOU KNOW?

Refraction of light is necessary for proper image formation; that is, refraction of light helps our eyes focus an image on the retina. As light enters the eye, it passes from a medium with an index of refraction of 1.00 (air) to a structure with a refraction index of 1.38 (the cornea). The difference between these two media makes the light rays bend significantly. The refractive index of the aqueous humor is 1.33, close to that of the cornea and, therefore, it does not greatly alter the path of light after it leaves the cornea. The lens has a refractive index of 1.40, slightly higher than that of the aqueous humor. Thus, it is actually the cornea that refracts most of the light that strikes the eye. However, the lens's refractive abilities are needed for fine-tuning an image, especially as you shift your focus between distant and near objects. The importance of the cornea's ability to refract light can be observed when you open your eyes under water. You cannot see clearly under water because the cornea's refractive index is very close to that of water, so light is essentially passing from one watery medium to another. To increase the difference between the cornea and the water and see more clearly, you can wear goggles or a face mask.

FOCUSING OF LIGHT

The lens of the eye functions like a camera lens. It is **convex** in shape—that is, it is thickest in the middle. The shape of the lens allows it to bend light rays so they meet at a single spot on the retina, called the **focal point**. The distance between the center of the lens and its focal point is the **focal distance**. The focal distance is determined by two important factors: how far an object is from the lens and the shape of the lens. For instance, the focal distance increases as an object moves closer to the lens. In addition, the thicker the lens, the more light will be bent, which will shorten the focal distance. The powers of the cornea and humors (aqueous and vitreous) to refract light are constant. However, the lens is highly elastic, so its curvature can be changed. This, in turn, alters its refractive power, to allow the eye to finely focus an image.

FOCUSING FOR DISTANT VISION

Our eyes are actually best adapted for distant vision. This means that the lens does not have to change in shape when we look at a distant object. For a normal eye, the distance beyond which no change in lens shape is necessary is about 6 m (roughly 20 ft). This is because, beyond that point, light approaches the eyes as nearly parallel rays and can be focused on the retina by the fixed refractory structures (the cornea and humors). When we look at a distant object, the ciliary muscles will relax, which allows the elastic lens to be stretched flat, providing the least ability to refract.

FOCUSING FOR CLOSE VISION

The lens must make adjustments for close vision (less than 6 m, or about 20 ft, away) because light rays from a close object diverge as they approach the eyes. In fact, close vision requires three adjustments to be made at the same time: (1) constriction

of the pupils, which limits the divergence of light rays, forcing them to pass though the center of the lens; (2) convergence of the eyeballs; and (3) accommodation of the lens. **Accommodation** refers to the lens's ability to change its shape in order to keep the focal length constant.

During accommodation, the lens gets rounder. This, in turn, increases its refractory power, enabling it to focus a nearby image on the retina. Accommodation is done through contraction of the ciliary muscles, which allows the elastic lens to become more spherical in shape. For normal vision (**emmetropia**), the lens is about 3.6 mm (0.14 in) thick. In contrast, during accommodation, the lens thickens to about 4.5 mm (0.18 in). One consequence of reading or other close work is that it requires almost continuous accommodation, pupillary constriction, and eye convergence. This explains why prolonged periods of reading tire the eye muscles and can result in eyestrain.

The closest point on which we can focus clearly is limited by the maximum bulge the lens can achieve. This is determined by the degree of elasticity in the lens, which decreases with age. Children can usually focus on something 7 to 9 mm (less than 1 in) from the eye. However, as we get older, the lens tends to become stiffer and less responsive. A young adult may be able to focus on objects about 15 to 20 mm (0.6 to 0.8 in) away, but by the time we reach the age of 50 or 60 years, the lens essentially loses the ability to accommodate, a condition known as presbyopia. In this case, the near point is typically about 80 cm (32 in), which explains why most older people require reading glasses.

ANATOMY OF RODS AND CONES

Light is focused on the retina in order to stimulate photoreceptor cells. Both rods and cones have a similar structure in that they have an outer and an inner segment. The

YOUR HEALTH: Myopia and Hyperopia

Visual problems related to refraction can result from structural abnormalities of the eyeball (Figure 7.1). For instance, if the eyeball is too deep or if the resting curvature of the lens is too great, the image of a distant object will form in front of the retina. This will cause the individual to see distant objects as blurry, but the person's vision will be normal at close range because the lens is able to accommodate. This condition is known as **myopia**, or nearsightedness. Myopia can be treated with eyeglasses that have a diverging (concave) lens. In addition, a short laser surgery (radial keratotomy or LASIK) can be used to flatten the cornea slightly, which decreases its refractive properties.

In contrast to myopia, **hyperopia**, or farsightedness, occurs when the eyeball is too shallow or the lens too flat. In this case, parallel rays of light are focused behind the retina. People with hyperopia can see distant objects well. However, the lens cannot provide enough refraction power at close range. This is because the diverging light rays of a nearby object are focused so far behind the retina that the lens cannot bring the focal point onto the retina even at its full refractory power. Hyperopia can be corrected by eyeglasses with a converging (convex) lens.

Finally, **astigmatism** occurs when the cornea or lens fails to refract light properly, which can distort the visual image. This usually happens when the degree of curvature in the cornea or lens varies from one axis to another. For instance, the vertical axis may be more strongly curved than the horizontal axis. Luckily, this visual problem can be corrected with eyeglasses or special contact lenses.

YOUR HEALTH: Myopia and Hyperopia *(continued)*

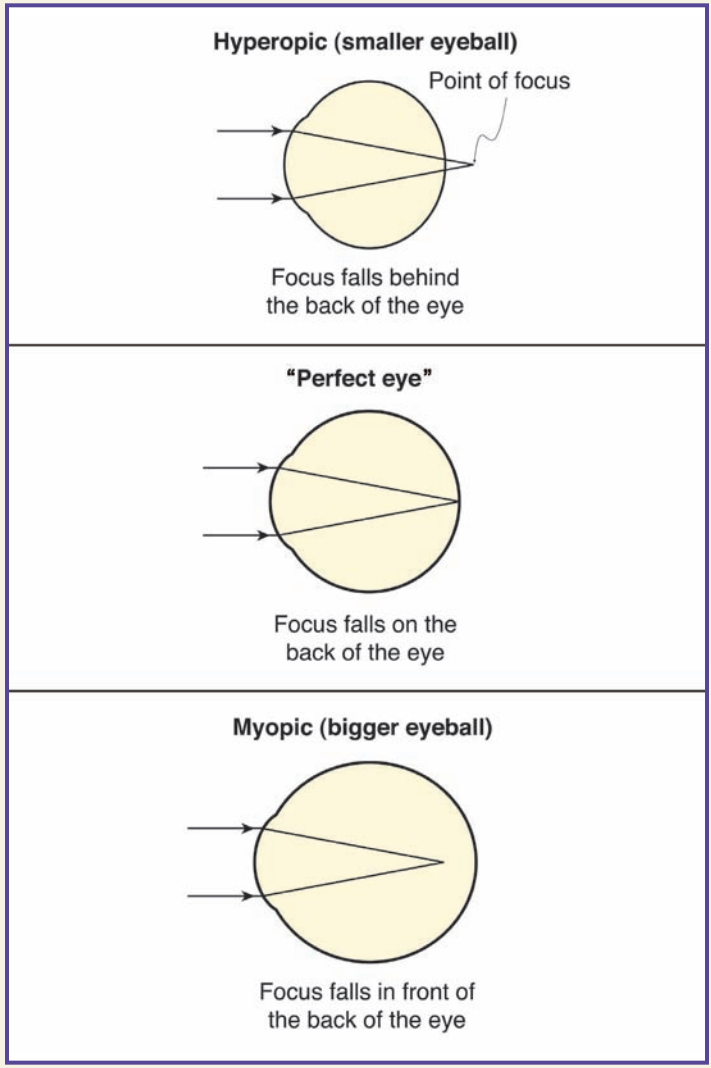
Hyperopic (smaller eyeball)
Point of focus
Focus falls behind the back of the eye
"Perfect eye"
Focus falls on the back of the eye
Myopic (bigger eyeball)
Focus falls in front of the back of the eye

Figure 7.1 Light rays entering an eye are refracted (focused) by the cornea and lens so they meet on the retina. However, when a person has myopia (nearsightedness), the eyeball is too long. This causes light rays to meet before they reach the retina. In contrast, hyperopia (farsightedness) causes light rays to meet behind the retina.

outer segment is the receptor region, essentially a highly modified cilium specialized to absorb light. This specialization includes hundreds to thousands of flattened membrane plates or disks, which dramatically increase the membrane surface area. The names "rod" and "cone" refer to the shape of the outer segment when viewed under a microscope: In rods, the outer segment is slender and rod-shaped; in cones, it is shorter and conical. The **inner segment** of both photoreceptors is connected to the outer segment by a narrow connecting stalk. The inner segment corresponds to the cell body of a nerve cell and contains all the usual cellular organelles, including a nucleus. It makes contact with other cells in the retina.

Rods and cones are "wired" to other retinal neurons differently. For instance, up to 100 rods may connect to a single ganglion cell. As a result, the output of rods is considered as a whole, which leads to vision that is fuzzy

DID YOU KNOW?

Visual acuity is a measure of the resolving power of the eye rated against a standard of 20/20 vision. A person with 20/20 vision can see details at a distance of 20 feet. An individual is considered to have better than average vision if he or she can see detail at a distance greater than 20 feet. For instance, 20/15 vision indicates that a person can see items at a distance of 20 feet that would be clear to a normal eye at a distance no farther than 15 feet. In contrast, a person with 20/30 vision must be 20 feet from an object to see the detail that a normal person could make out at a distance of 30 feet. A person is considered legally blind when visual acuity is worse than 20/200. Sometimes visual acuity is affected by floaters, small spots that drift across the field of vision. They are generally temporary phenomena resulting from blood cells or cellular debris floating within the vitreous humor.

and indistinct. In contrast, each cone in the fovea has a single, straight pathway to a ganglion cell. As a result, each cone essentially has its own "labeled line" to the higher visual centers.

VISUAL PIGMENTS

The disks of the outer segment of rods and cones contain special organic compounds called **visual pigments** that change shape when they absorb light. The absorption of photons by visual pigments is the first step in the process of photoreception. The visual pigment found in rods is called **rhodopsin**, or visual purple, because it initially takes on a deep purple color when exposed to light. Rhodopsin consists of two major parts: an **opsin** protein bound to the pigment **retinal**, which is made from vitamin A. Although rhodopsin absorbs all wavelengths of visible light, it has a peak absorption at 500 nm (green), and neural inputs from rods are only perceived in gray tones.

The visual pigments of cones all have the same retinal pigment as rods. However, the retinal is attached to different forms of opsin, and the various forms of opsin are composed of different sequences of amino acids, which determine the wavelengths of light that can be absorbed by the retinal pigment. Human beings have three different kinds of cones that are identical in appearance, but they absorb different wavelengths of light. It is the differential stimulation of populations of cones by light that is the basis of color vision.

PHOTORECEPTION IN RODS

Retinal can take on two distinct three-dimensional shapes. In darkness and when retinal is bound to opsin, it has a bent shape and is known as the ***cis*-retinal**. However, when retinal absorbs the energy of a photon of light, it is converted to a straight form called the ***trans*-retinal**. Amazingly, the change from *cis*- to *trans*-retinal is the only light-dependent step

in photoreception and is responsible for initiating several enzymatic steps that ultimately lead to electrical events resulting in vision.

Rhodopsin accumulates in the dark. It is arranged in a single layer in the membranes of each disk in the outer segments of rods. When rhodopsin absorbs light, it quickly fades to a colorless compound, a process called bleaching. Bleaching results from the conversion of retinal to its *trans* form. When this occurs, the *trans*-retinal physically separates from the opsin protein and is transported to the pigment epithelium at the back of the retina. The *trans*-retinal is converted back to *cis*-retinal in an energy-requiring process, which is then transported to the rod outer segment and reunited with opsin.

What is the significance of separating *trans*-retinal from opsin? The freed opsin is able to activate an enzyme that in turn causes the closing of Na^+ channels, decreasing the rate of Na^+ entry into the cell, and thereby hyperpolarizing the cell membrane. As the photoreceptor membrane hyperpolarizes, the rate at which neurotransmitter (chemical messengers) release decreases, which is the signal to bipolar cells that the photoreceptor has absorbed a photon.

For a rod to continue to function, it must regenerate rhodopsin at a rate that keeps pace with bleaching. It takes about 5 minutes to regenerate 50% of the bleached rhodopsin. Thus, bleaching contributes to the lingering visual impression after a camera's flash goes off. That is, after an intense exposure to light, a photoreceptor cannot respond to further stimulation until its rhodopsin molecules have been regenerated. Bleaching is seldom noticed under ordinary circumstances because the eyes are constantly making small involuntary changes in position that move the image across the retinal surface. In addition, because cones are less dependent on the pigment epithelium, they can regenerate half their pigment in about 90 seconds.

COLOR VISION

Most nocturnal vertebrates (animals that are active at night) have only rods. However, many animals that are active during the day have cones and, therefore, color vision. Humans have three types of cones, each with its own visual pigment. Although the retinal is the same for all three cones, their opsins differ. The name of a specific cone reflects the wavelengths (colors) of light it absorbs best. **Blue cones** respond best to wavelengths of light around 420 nm, **green cones** to wavelengths around 530 nm, and **red cones** to wavelengths around 565 nm (Figure 7.2). The wavelengths of light absorbed by the three types of cones overlap, and we perceive hues such as orange, yellow, and purple when more than one cone is activated at the same time. For instance, yellow light causes a combination of inputs from green cones (highly stimulated), red cones (somewhat stimulated), and blue cones (relatively unaffected). An object appears to have a particular color because it reflects (transmits) photons from one portion of

DID YOU KNOW?

Retinal is made from vitamin A. The pigmented layer in the sensory tunic stores vitamin A, and the body as a whole has enough vitamin A to last for several months. However, if you don't get enough vitamin A in your diet, your amount of visual pigment can decrease. Although daylight vision is affected, ambient light (the light in the environment around us) is usually bright enough to stimulate whatever visual pigments remain within the cones. On the other hand, exposure to dim light may not be enough to activate rods, causing a condition known as night blindness. Night blindness can dramatically impair a person's ability to drive safely in the dark. Vitamin A supplements can restore function if they are taken before the vision has actually degenerated. Carrots are a very good source of vitamin A, which explains why people often say that carrots are good for your eyes.

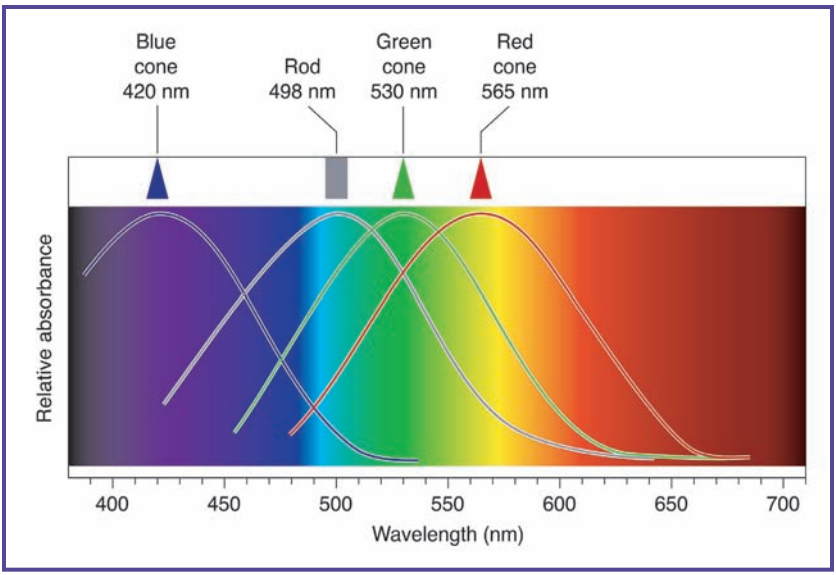

Figure 7.2 **Photoreceptors contain unique visual pigments. As a result, they absorb different wavelengths of light and have different thresholds for activation. This chart shows the wavelengths to which each type of cone—blue, green, and red—responds best.**

the visible spectrum and absorbs the rest, and it is those reflected photons that stimulate the cones. If photons of all colors bounce off an object, and all cones are stimulated equally, we see white. In contrast, if all the photons are absorbed by a specific object, so that none reaches the retina, it will appear black.

LIGHT AND DARK ADAPTATION

An important adaptation of our visual system is the ability to adjust its sensitivity to light with changes in the intensity of illumination. For instance, in low-intensity light, relatively little rhodopsin is bleached and the retina can respond continuously to stimuli. However, if you go from a dark room into a brightly lit area, there will be a massive bleaching of visual pigments, causing the light to seem unbearably bright. At this point, rods essentially become nonfunctional.

In response, pupils quickly constrict to reduce the intensity of stimulation. Soon, color vision and visual acuity develop, a phenomenon known as **light adaptation**. Within about 60 seconds, cones are sufficiently excited by bright light to take over, although they may not work at full capacity for 5 to 10 minutes, the time needed for pigment bleaching to adjust retinal sensitivity to this new light intensity. Therefore, during light adaptation, rod function is lost, but visual acuity is gained.

In contrast, **dark adaptation** is needed when you move from a well-lit area to a dark room. Dark adaptation is essentially the reverse of light adaptation. At first, we see nothing because our cones stop functioning in low-intensity light and our rods' pigments are still in a bleached state from the previous bright light. However, once in the dark, rhodopsin accumulates as it regenerates faster than it is bleached, and the sensitivity of rods begins to increase. Dark adaptation is slower than light adaptation, and can continue for several hours (although, typically, within 20 to 30 minutes, the amount of rhodopsin regenerated is sufficient to have reached almost the maximum possible sensitivity in dark). The visual system also responds by dilating pupils, which helps let more light into the eyes. When fully dark-adapted, the

YOUR HEALTH: Color Blindness

People who are unable to distinguish certain colors are considered color blind. This condition results from a sex-linked inherited lack of one or more of the cone types. About 8 to 10% of males and about 0.5% of females have some form of color blindness. The most common type is red-green color blindness, resulting from an absence of either red or green cones. In this case, red and green are seen as the same color—either red or green, depending on the type of cone that is present.

visual system is extremely sensitive. For instance, a single rod will hyperpolarize in response to a single photon of light, and as few as seven rods absorbing photons at one time will be perceived as a flash of light. In addition to the above, there are a variety of central nervous system responses to further adjust light sensitivity for different conditions. Altogether, the entire system may increase its efficiency by a factor of more than 1 million.

CONNECTIONS

Our eyes respond to the part of the electromagnetic spectrum called visible light. Light is actually composed of small packets of energy called photons. The speed of light is constant in a given medium; however, when it passes through one transparent medium into another with different density, its speed changes. These changes of speed cause light to bend or refract when it meets the surface of a different medium at an oblique angle.

The lens of the eye is convex, which bends the light rays so they converge at a single point on the retina called the focal point. The distance between the center of the lens and its focal point is called the focal distance. Although the refractory power of the cornea and humors are constant, the lens is highly elastic, and its curvature can be changed. This, in turn, changes its refractive power so that fine focusing of an image can occur.

Our eyes are actually best adapted for distant vision. For a normal eye, the far point of vision is 6 m (about 20 ft). The lens must make adjustments for close vision, which requires three simultaneous changes: constriction of the pupils, convergence of the eyeballs, and accommodation of the lens. Accommodation refers to the ability of the lens to change its shape in order to keep the focal length constant. The closest point on which we can focus clearly is called the near point of vision. It is limited by the maximum bulge the lens can achieve, and is determined by

the degree of elasticity in the lens. By the age of 50 or 60, the lens no longer accommodates, a condition known as presbyopia.

Light is focused on the retina in order to stimulate photoreceptor cells. Both rods and cones have an outer segment and an inner segment. The outer segment is the receptor region and contains flattened membrane disks, which have visual pigment molecules that can change their shape when they absorb light. The inner segment of both photoreceptors makes contact with other cells in the retina. The disks of the outer segment of rods and cones contain special organic compounds called visual pigments. The absorption of photons by visual pigments is the first step in the process of photoreception. Visual pigments are derived from the compound rhodopsin, which consists of an opsin protein bound to the pigment retinal. Cones have the same retinal pigment as rods, but different forms of opsin. Retinal can assume two distinct three-dimensional shapes. In darkness and when bound to opsin, retinal has a bent shape and is called *cis*-retinal. However, when retinal absorbs the energy of a photon of light, it is converted to a straight form called *trans*-retinal. This process, called bleaching, involves the separated *trans*-retinal being transported to the pigment epithelium at the rear of the retina. It is then converted again to *cis*-retinal, in an energy-requiring process, transported back to the rod outer segment, and reunited with opsin.

The freed opsin following bleaching is able to activate enzymes that help hyperpolarize the cell membrane. As the membrane hyperpolarizes, the rate of neurotransmitter release decreases, telling bipolar cells that the photoreceptor has absorbed a photon.

Humans have three types of cone cells—blue, green, and red—and the name of each cone reflects the wavelengths of light each absorbs best. The wavelengths of light absorbed by the three cones overlap, and perception of hues results when more than one cone is activated at the same time.

The sensitivity of our visual system varies with the intensity of illumination. Light adaptation occurs when you go from a dark room into bright light; dark adaptation is needed when you move from a well-lit area to a dark room.

8

Sense of Hearing

The sense of hearing allows us to detect and interpret sound waves, which result from vibrating air molecules. This sense is necessary in normal human life because hearing and speech are important means of communication and the basis of complex social interactions. In fact, a loss of hearing can result in unfortunate behavioral disturbances.

PROPERTIES OF SOUND

Sound, defined as any audible vibration of molecules, is essentially made up of pressure disturbances that consist of alternating areas of high and low pressure. Because sound depends on vibrating molecules, it cannot be sent through a vacuum like light, but can be transmitted though water, solids, and air. Sound also travels much more slowly than light does—about 331 m/sec (0.2 miles/sec) in dry air, compared to 300,000 km/sec (186,000 miles/sec) for light. For this reason, a lightning flash is seen almost instantly after it occurs, but the sound it creates (thunder) reaches our ears more slowly. In fact, each second that passes between a lightning bolt and its thunderclap indicates that a storm is about one-fifth of a mile farther away.

Sound is transmitted by a vibrating object, such as a tuning fork, loudspeaker, or vocal cords. For instance, if you strike a tuning fork, its prongs move back and forth. As the prongs move forward, they push air molecules closer together, producing a high-density area called a zone of compression. In contrast, as the prongs rebound, they create a less dense region called a zone of rarefaction. Thus, a vibrating object produces a series of compressions and

rarefactions, collectively called a **sound wave**, which moves outward in all directions. Individual molecules do not travel from the vibrating object to our eardrum. Instead, a molecule collides with its neighbor, and they create a ripple-like effect, similar to the surface of water when you throw a stone into it. The sensations we perceive as pitch and loudness of sound are related to the physical properties—the frequency and amplitude—of these vibrations.

PITCH

Frequency, expressed in **hertz** (Hz), or cycles per second, is defined as the number of waves that pass a given point over a period of time (Figure 8.1). The distance between two consecutive wave crests (or troughs) is called the **wavelength** of sound, and it is constant for a particular tone. For instance, the frequency of middle C on a piano is 261 Hz. Frequency and wavelength have inverse relationships. This means that the shorter the wavelength, the higher the frequency of a sound.

The human ear can hear frequencies between 20 and 20,000 Hz, and our ears are most sensitive to frequencies between 500 and 4,000 Hz (in that range, we can distinguish frequencies that differ by only 2 to 3 Hz). **Pitch** is our sense of whether a sound is high or low, and is determined by the frequency of sound waves. That is, the higher the frequency, the higher the pitch. Most sounds we hear are mixtures of several frequencies.

LOUDNESS

Loudness is the perception of sound energy—that is, the pressure difference between the compressed and rarefied areas. It is indicated by the **amplitude**, or the height of sound waves (refer again to Figure 8.1). Loudness is expressed in units called **decibels** (dB). By convention, 0 dB is arbitrarily set to be the threshold of human hearing. Every 10 dB step increase represents a sound that is 10 times more intense. For instance, 30 dB is 10 times louder than 20 dB and 100 times louder than 10 dB. Normal conversation is about 60 dB, and

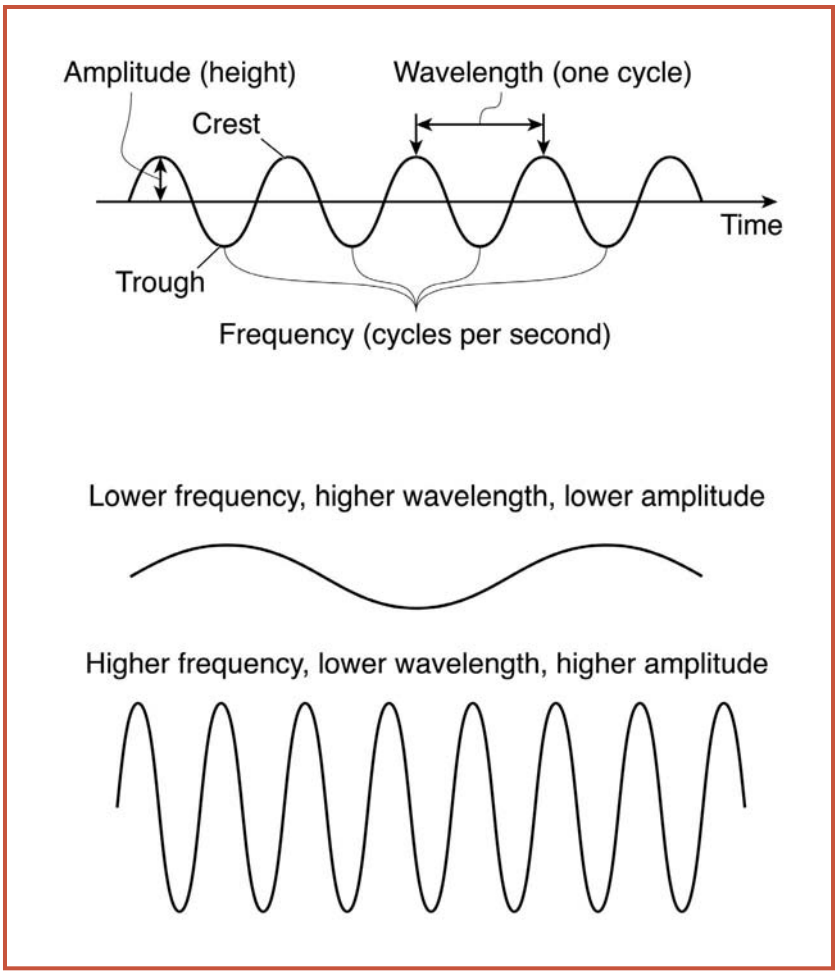

Figure 8.1 **A pure tone has periodic crests and troughs. The distance between two consecutive crests is called the wavelength, and it is constant for a specific tone. Frequency, expressed in hertz (Hz), is the number of waves that pass a certain point within a given time period (usually one second). The range of frequencies most humans can hear is from 20 to 20,000 Hz.**

the threshold for pain caused by sound is around 130 dB. Prolonged exposure to sounds greater than 90 dB can lead to permanent loss of hearing.

THE OUTER EAR

The ear is divided into three major regions: the outer ear, middle ear, and inner ear (Figure 8.2). The first two structures are only concerned with the transmission of sound to the inner ear, which houses the receptors that actually turn fluid motion into action potentials.

The **outer ear** is essentially a funnel for conducting air vibrations to the eardrum. It consists of the auricle, lobule, external auditory canal, and tympanic membrane. The **auricle** (or pinna) is the part that most people think of as the ear. It is composed of elastic cartilage covered with skin. The fleshy **lobule** (earlobe) lacks cartilage.

The **external auditory canal**, or ear canal, is a curved tube about 2.5 to 3 cm (about 1 in) long in adults. Although it is supported by cartilage at its opening, the remainder consists of a canal carved in the temporal bone. The canal is lined with skin bearing hair, sebaceous glands, and modified sweat glands called **ceruminous glands**. The secretions from these glands form a sticky, bitter substance called **cerumen**, or earwax, which traps foreign particles, repels insects, and slows the growth of microorganisms, thereby reducing the chance of infection. Normally, cerumen dries and falls from the canal. However, it sometimes becomes impacted and interferes with hearing.

Sound waves entering the canal eventually reach the **tympanic membrane**, or eardrum, which is a boundary between the outer and middle ear. This membrane is about 1 cm (less than half an inch) in diameter and is slightly concave on its outer surface, giving it a conical appearance. Sound waves make the eardrum vibrate, and the greater the intensity of sound, the further the membrane is displaced.

THE MIDDLE EAR

The **middle ear**, a small, air-filled space, is located in the **tympanic cavity** of the temporal bone. The anterior wall of the

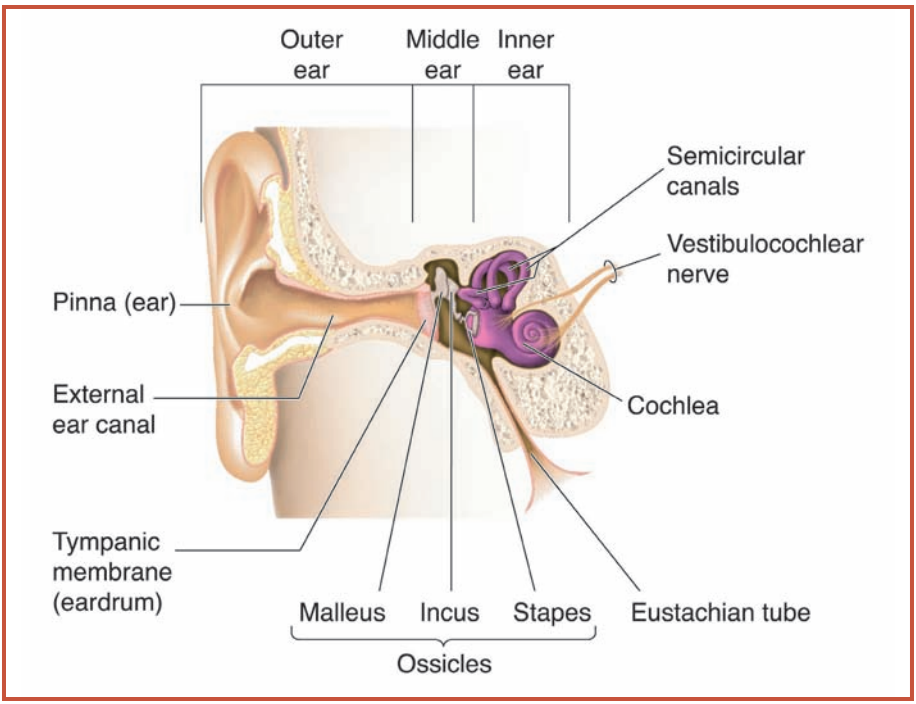

Figure 8.2 **The outer ear funnels sound waves into the external ear canal. The tiny bones, or ossicles, of the middle ear act as a lever system, raising the pressure exerted on the oval window—the place where the inner ear begins. The inner ear contains the cochlea, a structure that turns pressure waves into electrical signals that allow us to perceive sound.**

middle ear contains the opening of the **auditory tube** (or Eustachian tube), a passageway to the area of the upper throat behind the ear. Normally, this tube is flattened and closed. However, swallowing and yawning opens it briefly and allows air to enter or leave the tympanic cavity, which makes the pressure on both sides of the eardrum equal. This is important because the eardrum does not vibrate freely unless the pressure of both of its surfaces is the same. You may notice the "ear-popping" sensation of pressure equalizing when you fly on an airplane and it changes altitude.

The middle ear also contains the three smallest bones in the human body, which span the 2- to 3-mm distance from the eardrum to the inner ear. The bones are called **ossicles**, and are named for their shapes. The **malleus**, or hammer, is attached to the inner surface of the eardrum and joins with the **incus** (the anvil), which, in turn, joins with the **stapes** (the stirrup). The base of the stapes fits into the **oval window**, where the inner ear begins. The function of the ossicles is to transmit the vibrating motion of the eardrum to the oval window. Because the tympanic membrane is about 20 times larger in diameter than the oval window, a movement in the tympanic membrane produces a 20 times larger deflection at the base of the stapes.

Two tiny skeletal muscles associated with the ossicles are also found in the middle ear. The **tensor tympani** comes out of the wall of the auditory tube and attaches to the malleus, while the **stapedius** originates from the rear wall of the cavity and joins with the stapes. When the ears are exposed to very loud sounds, these muscles contract reflexively to prevent damage to the hearing receptors in the inner ear. In particular, the tensor tympani tenses the eardrum and the stapedius limits the vibration of the whole ossicle chain, thereby limiting the movement of the stapes on the oval window. This reflex probably evolved in part for protection

YOUR HEALTH: Middle Ear Problems

A middle ear inflammation (otitis media) is a fairly common result of a sore throat, especially in children, whose auditory tubes are shorter and run more horizontally than those of adults. Otitis media is the most common cause of hearing loss in children; cases are often treated with antibiotics. Tinnitus is the sensation of a ringing or clicking sound in the ears when no outside sound really exists. It can be a symptom of nerve denegation, the result of otitis media, or a side effect of some medications, such as aspirin.

from loud but slowly developing noises, such as thunder, because it has a latency period of about 40 milliseconds (msec), which is not quick enough to protect the inner ear from sudden noises such as gunshots.

THE INNER EAR

The **inner ear** is housed deep within the temporal bone and contains receptors for the senses of hearing and equilibrium (equilibrium will be discussed in Chapter 9). The inner ear has two major divisions: the bony labyrinth and the membranous labyrinth. The **bony labyrinth** is a maze of passageways in the temporal bone. It has three regions: the vestibule, cochlea, and semicircular canals (only the cochlea will be discussed here; the other two structures have to do with the sense of equilibrium).

The **membranous labyrinth** is a continuous series of fluid-filled membranous sacs and ducts inside the bony labyrinth. The fluid in the membranous labyrinth, called **endolymph**, has different electrolytes in it, compared to most other body fluids. It is high in potassium and low in sodium. Between the bony and membranous labyrinths is a cushion of fluid called the **perilymph**. Together, endolymph and perilymph are responsible for conducting the sound vibrations involved in hearing.

The **cochlea** (Latin for "snail") is a spiral, cone-shaped bony chamber about half the size of a garden pea (Figure 8.3a). Its outer shell makes 2.5 turns around a central bony pillar, giving it a snail-like appearance. The cochlea has three fluid-filled chambers, called scala, separated by membranes (Figure 8.3b). Running through the center of the cochlea is a worm-like chamber called the **scala media**, which ends blindly at the cochlear apex. The scala media houses the **organ of Corti**, which is the actual receptor organ for the sense of hearing. The superior chamber in the cochlea is called the **scala vestibuli**. It connects with the oval window. Finally, the inferior chamber, the **scala tympani**, ends at the **round window**, the membrane

that separates the inner ear from the middle ear. Because the scala media is part of the membranous labyrinth, it is filled with endolymph. However, the scala vestibuli and scala tympani are part of the bony labyrinth and thus contain perilymph. These two chambers communicate with each other through a narrow channel at the cochlear apex.

The scala media is separated from the scala vestibuli above by a thin **vestibular membrane** and is separated from the scala tympani below by a much thicker **basilar membrane**, which supports the organ of Corti. The basilar membrane is narrow and thick near the oval window, and gradually becomes wider and thinner as it approaches the cochlear apex. This structural change is important for sound reception.

The organ of Corti converts sound vibrations into nerve impulses (Figure 8.3c). It has an epithelium made of four rows of **hair cells** and supporting cells. Hair cells get their name from the long, stiff microvilli at their top, called **stereocilia**. Hair cells are not neurons, but rather synapses with nerve fibers at their base. The hair cells are arranged by function, with about 3,500 **inner hair cells** forming a single row. Each of these hair cells has a cluster of 50 to 60 stereocilia, arranged from short to tall. Approximately 12,000–20,000 **outer hair cells** form three rows across from the inner hair cells. Each outer hair cell has about 100 stereocilia grouped in the shape of the letter "V." Resting on top of the stereocilia is a gelatinous **tectorial membrane**, and the entire structure sits on top of the basilar membrane. The stereocilia thus protrude into the K^+-rich endolymph, and the longest of them are embedded in the overlying tectorial membrane. It turns out that what we hear only comes from the inner hair cells that send their signals by means of sensory nerve fibers of the cochlear nerve, which runs from the organ of Corti to the brain. The outer hair cells adjust the response of the cochlea to different frequencies, which lets the inner hair cells work with greater precision.

TRANSMISSION OF SOUND TO THE INNER EAR

Before describing the physiology of hearing, which involves exciting the hair cells in the organ of Corti, it is essential to discuss how sound is transmitted. Airborne sound enters the external auditory canal and strikes the tympanic membrane. This causes the membrane to vibrate at the same frequency, and the amplitude of this vibration depends on how intense the sound is. The motion of the eardrum is then transmitted to the oval window through the middle ear ossicles.

One might ask why sound waves don't hit the oval window directly—that is, why do we need ossicles? The answer has to do with the fluid-filled chambers behind the oval window. The eardrum vibrates easily because it is surrounded by air. In contrast, the oval window has to vibrate against the fluid of the inner ear. Because this fluid puts up a much greater resistance to motion than air does, if sound waves struck the oval window directly, there would not be enough energy to overcome the resistance.

The ossicles, which act as a system of pistons, transfer the same total force that hits the tympanic membrane to the oval window. However, because the tympanic membrane is about 20 times larger than the oval window, the pressure per unit area exerted on the oval window is about 20 times that on the eardrum. This increased pressure overcomes the resistance of the cochlear fluid, making it vibrate. As mentioned earlier, the ossicles also help protect the ear in response to a loud noise (through the action of two tiny skeletal muscles). The middle ear muscles also help coordinate speech with hearing. Without them, the sound of our own speech would be so loud that it could damage the inner ear. To prevent this, just as we are about to speak, the brain signals these muscles to contract.

As the stapes rocks back and forth against the oval window, it sets the perilymph in the scala vestibuli into a similar motion. In this way, pressure waves travel through the perilymph from the basal end toward the narrow channel at

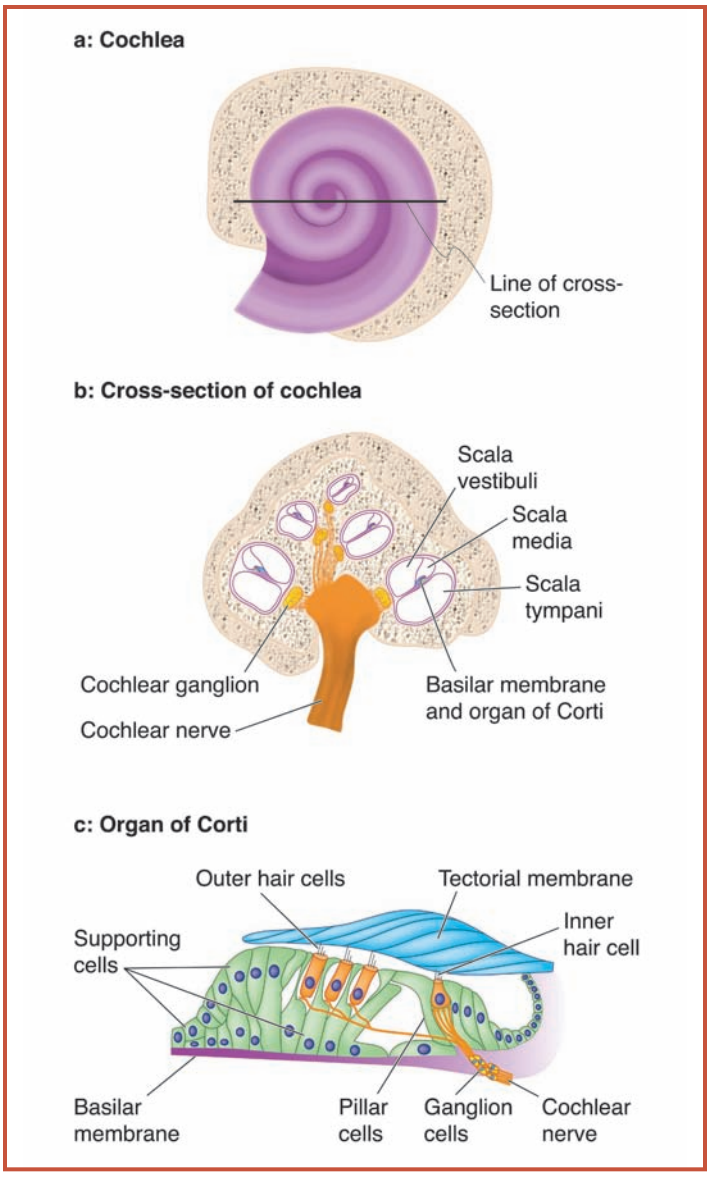

Figure 8.3 The organ of Corti, which is housed inside the cochlea (a and b), is the receptor organ for hearing. It is made up of supporting cells and about 20,000 hearing receptor cells called hair cells, all of which play specialized roles in the sense of hearing.

the cochlear apex. Sounds of low frequency (below 20 Hz) create pressure waves that go all the way through the perilymph of the cochlea to the round window. Such sounds do not activate the organ of Corti because they are below the threshold of hearing. However, sounds of higher frequency create pressure waves that go through the scala media into the perilymph of the scala tympani. As these pressure waves move through the scala media, they make the basilar membrane vibrate, thereby exciting the organ of Corti. Each time this occurs, the pressure waves make the round window bulge into the middle ear cavity, which acts like a pressure valve, dissipating the fluid vibration. This prevents us from hearing an echoing sound every time we hear something.

YOUR HEALTH: Deafness

Any hearing loss is considered deafness. However, there are two types of deafness—conduction deafness and sensorineural deafness—which differ in their causes. Conduction deafness occurs when sound transmission (conductance) has trouble reaching the fluids of the inner ear. This can result from a buildup of earwax or a ruptured eardrum. However, the two most common causes are middle ear inflammations and otosclerosis of the ossicles. Otosclerosis happens when too much bony tissue grows and fuses the stapes to the oval window or fuses the ossicles to one another. This condition can be treated with a hearing aid or surgery.

Sensorineural deafness happens when neural structures, including hair cells, cochlear nerve fibers, and auditory brain cells, get damaged. For instance, being exposed for a long time to high-intensity sound, such as jet engines, makes the stereocilia stiffen and tear. Sensorineural deafness also can happen when the cochlear nerve degenerates, or if a person suffers a stroke or a brain tumor. Some of these conditions may be treated with a cochlear implant, which converts sound energy to electrical signals, bypassing the organ of Corti, and sends them directly to the appropriate region of the brain.

PHYSIOLOGY OF HEARING

To produce a sensation of sound, the hair cells of the organ of Corti must be excited. This happens when pressure waves are transmitted through the scala media, which causes the basilar membrane to vibrate. Keep in mind that the tips of the longest stereocilia of hair cells are embedded in the tectorial membrane, which is anchored in place. As a result, the tectorial membrane remains relatively still as the basilar membrane and hair cells vibrate up and down. Consequently, as it moves, the basilar membrane bends the stereocilia back and forth, pressing them against the tectorial membrane.

Sound stimuli turn into voltage when the stereocilia are deflected by movements of the basilar membrane. This is possible because the tips of stereocilia of inner hair cells contain proteins that work as mechanically gated ion channels (passageways that open when the stereocilia bend). In addition, a fine protein filament called a tip link extends like a spring from an ion channel of a stereocilium to one next to it. So, when a taller stereocilium bends away from a short one, it pulls on the tip link, which opens the ion channel of the shorter stereocilium.

The most common ion in endolymph is K^+ (potassium). Consequently, when these channels are opened, they cause an inward K^+ current, which depolarizes the hair cell. In contrast, when the stereocilium bends the other way, its channel closes, and the cell repolarizes. Depolarization makes a hair cell release more neurotransmitter, which stimulates the sensory dendrites at its base. This, in turn, causes the cochlear fibers to send a faster stream of impulses to the brain.

As mentioned above, the basilar membrane is not uniform in shape. It is narrower and thicker near the oval window. It also has collagen fibers that span its width, similar to strings of a piano or harp. This arrangement gives the entire structure different resonant properties along its length. As a result, the membrane is displaced most at the point where its fibers are

most "tuned" to a particular sound frequency. For instance, fibers near the oval window are short and stiff, so they resonate in response to high-frequency pressure waves. The longer, floppier basilar membrane fibers near the cochlear apex, on the other hand, resonate in time with lower-frequency pressure waves. In this way, the basilar membrane mechanically processes sound signals before they reach the receptors, the hair cells of the organ of Corti.

SENSORY CODING

We are able to distinguish pitch and loudness, and to figure out where a sound is coming from. The perception of pitch results from the properties of the resonance basilar membrane, which allows the hair cells in different parts of the organ of Corti to be activated by sound waves of different frequencies. Impulses from specific hair cells are then interpreted as particular pitches by the auditory cortex in the brain. When a sound is made up of tones of many frequencies, several groups of hair cells are activated at the same time.

Our perception of loudness is a result of louder sounds producing more vigorous vibrations of the organ of Corti. This, in turn, excites a larger number of hair cells over a broader area of basilar membrane, triggering a higher frequency of action potentials in the cochlear nerve fibers. Determining the source of sound occurs by means of two cues: the relative intensity and the relative timing of sound waves reaching the two ears.

CONNECTIONS

Sound, defined as any audible vibration of molecules, is essentially made up of pressure disturbances that have alternating areas of high and low pressure. Sound can be transmitted though water, solids, and air, and travels much more slowly than light. A vibrating object produces a series of compressions and rarefactions, collectively called a sound wave, which moves outward in all directions. The sensations we perceive as pitch

and loudness of sound are related to the physical properties of these vibrations.

Sound can be described in terms of two physical properties: frequency and amplitude. Frequency, expressed in hertz (cycles per second), is the number of waves that pass a given point over a period of time. The distance between two consecutive wave crests (or troughs) is called the wavelength of sound and it is constant for a particular tone. Pitch is our sense of whether a sound is high or low, and is determined by the frequency of sound waves. Loudness is the perception of sound energy and is indicated by the amplitude or height of sound waves. Loudness is expressed in units called decibels (dB).

The ear has three major regions: the outer ear, middle ear, and inner ear. The outer ear is essentially a funnel that brings air vibrations to the eardrum. The auricle is what most people think of as the ear—the outer structure composed of cartilage covered by skin, along with the fleshy earlobe called the lobule. The external auditory canal, or ear canal, is a curved tube that has modified apocrine sweat glands called ceruminous glands. Cerumen (earwax) traps foreign particles, repels insects, and slows the growth of microorganisms. The tympanic membrane (eardrum) forms a boundary between the outer and middle ear.

The middle ear is located in the tympanic cavity of the temporal bone. The anterior wall of the middle ear contains the opening of the auditory (eustachian) tube, a passageway to the top of the throat. The middle ear also contains ossicles: the malleus (hammer), incus (anvil), and stapes (stirrup). The base of the stapes fits into the oval window, where the inner ear begins. The function of the ossicles is to transmit the vibratory motion of the eardrum to the oval window. Two tiny skeletal muscles associated with the ossicles—the tensor tympani and stapedius—contract reflexively when exposed to loud sounds to prevent damage to the hearing receptors in the inner ear.

The inner ear is housed deep within the temporal bone and contains receptors for the senses of hearing and equilibrium. It has two major parts: the bony labyrinth and the membranous labyrinth. The bony labyrinth has three regions: the vestibule, cochlea, and semicircular canal. The membranous labyrinth is a continuous series of fluid-filled membranous sacs and ducts held within the bony labyrinth. The fluid inside the membranous labyrinth is called endolymph. Between the bony and membranous labyrinths is a cushion of fluid called the perilymph.

The cochlea is a spiral, conical bony chamber with three fluid-filled chambers, called scala, separated by membranes. Running through the center of the cochlea is a worm-like chamber called the scala media of the membranous labyrinth, which ends blindly at the cochlear apex. The scala media houses the organ of Corti. This is the actual receptor organ for the sense of hearing. The superior chamber in the cochlea is called the scala vestibuli. It connects with the oval window. The inferior chamber, the scala tympani, ends at the round window. The scala media is separated from the scala vestibuli above by a thin vestibular membrane and is separated from the scala tympani below by a much thicker basilar membrane, which supports the organ of Corti.

The organ of Corti is composed of four rows of hair cells with stereocilia on their apical surface. Resting on top of the stereocilia is a gelatinous tectorial membrane, and the entire structure sits on top of the basilar membrane. The stereocilia stick out into the K^+-rich endolymph. The longest ones are embedded in the overlying tectorial membrane. The inner hair cells send their signals via the sensory nerve fibers of the cochlear nerve. The function of the outer hair cells is to adjust the response of the cochlea to different frequencies, which enables the inner hair cells to work with greater precision.

The eardrum vibrates easily because it is in air. The ossicles, which act as a system of pistons, transfer the force

hitting the tympanic membrane to the oval window. Because the tympanic membrane is about 20 times larger than the oval window, the pressure per unit area exerted on the oval window is about 20 times that on the eardrum.

To produce a sensation of sound, the hair cells of the organ of Corti must be excited. This happens when pressure waves are transmitted through the scala media, which cause the basilar membrane to vibrate. Movement of the basilar membrane bends the stereocilia back and forth as they are pressed against the tectorial membrane.

Transduction of sound stimuli occurs after the stereocilia are deflected by localized movements of the basilar membrane. At the tips of the stereocilia of inner hair cells are proteins that function as mechanically gated ion channels. When a taller stereocilium bends away from a short one, it pulls on the tip link, which opens the ion channel of the shorter stereocilium, causing a graded depolarization. Depolarization increases hair cells' release of neurotransmitter, which stimulates the sensory dendrites with their base.

The perception of pitch results from the properties of the basilar membrane, which allows for the activation of hair cells in different parts of the organ of Corti by sound waves of different frequencies. Impulses from specific hair cells are then interpreted as specific pitches by the auditory cortex in the brain. Localization of sound occurs by means of two cues: the relative intensity and the relative timing of sound waves reaching the two ears.

9

Sense of Equilibrium

The sense of equilibrium (balance and coordination) lets us detect the position of our head by monitoring gravity, linear acceleration, and rotation. Like the sense of hearing, equilibrium depends on mechanoreceptors (hair cells) located in the inner ear. In fact, the original function of the ear in vertebrates was for equilibrium, not hearing. During the course of evolution, the cochlea emerged, along with the middle ear structures, which allowed the ear to hear as well as maintain balance. The sense of equilibrium also depends on the sense of vision, as well as information from stretch receptors located in skeletal muscles and tendons.

STRUCTURE FOR SENSING EQUILIBRIUM

The receptors for sensing equilibrium are found in the **vestibular apparatus** of the inner ear (Figure 9.1). This structure consists of three semicircular ducts and two chambers: the anterior saccule and the posterior utricle. The **semicircular ducts** provide sensory information about rotational movements of the head, which is also referred to as **dynamic equilibrium**. For instance, when you turn your head to the right, stimulated receptors in the semicircular canals provide information about how fast the movement is and in which direction. The **saccule** and **utricle** send the brain signals about your position in space with respect to gravity, which is referred to as **static equilibrium**. For example, if you tilt your head

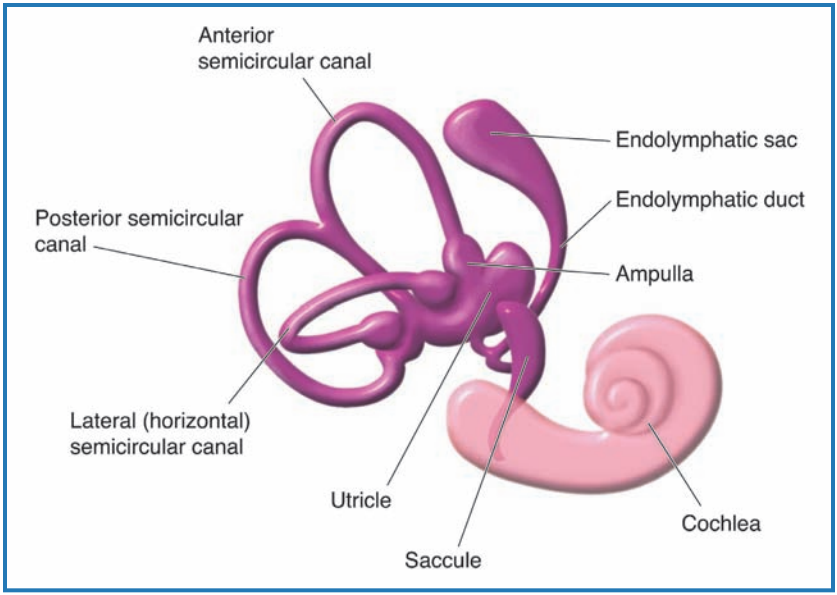

Figure 9.1 **The vestibular apparatus (seen here) is a part of the inner ear that gives us our sense of equilibrium (balance). The three semicircular canals react when we turn our head or change its angle. The utricle and saccule sense movement of the head because they notice changes in gravity. These equilibrium receptors give the brain information that it can use to determine the position and movement of the head and body.**

to one side, these receptors will provide information on the angle involved and whether your head is tilting forward, backward, or to one side. These receptors also are stimulated by sudden acceleration, such as when a car makes a "jack-rabbit" start. This lets us tell when we are moving faster physically.

THE SACCULE AND UTRICLE

The sensory receptors for static equilibrium are located in structures called **maculae** (singular is **macula**), which are found in the saccule and utricle. The **macula sacculi** lies nearly vertically in the wall of the saccule, and the **macula utriculi** lies almost horizontally on the floor of the utricle. These receptors take notice when our bodies move faster or slower in a forward or backward direction. They do not sense rotation, however.

They are important for monitoring the position of the head in space, and help us sense whether the body is moving.

Each macula is a flat epithelial patch (measuring about 2 by 3 mm) that contains supporting cells and scattered receptor cells (hair cells). Each hair cell has 40 to 70 stereocilia and one true cilium, called the **kinocilium**. The tips of the stereocilia and kinocilium are embedded in a jelly-like **otolithic membrane**. This membrane contains tiny calcium carbonate crystals called **otoliths** (literally, "ear stones"). These make the membrane denser and keep it still, which helps the recpetors notice changes in gravity and motion.

ACTIVATION OF MACULAE RECEPTORS

When your head is in the normal, upright position, otoliths sit on top of the macula utriculi and stimulation is minimal. However, when you tilt your head to one side, the weight of the otolithic membrane bends the stereocilia, which stimulates hair cells. Any orientation of the head causes a combination of stimulation of the utricles and saccules of the two ears. The brain figures out where the head is by comparing these inputs to each other and to other inputs from the eyes and stretch receptors. For instance, when you start to run, the

YOUR HEALTH: Dizziness

Besides holding the receptors for the sense of hearing, the inner ear plays an important role in the sense of equilibrium. Sometimes an infection or injury can impair the way the inner ear functions. Because receptors for equilibrium can be affected, symptoms of an inner ear infection can include dizziness and loss of balance. People often say they are "dizzy" when they feel "light-headed," but there is a difference. Dizziness is a more severe condition that involves a marked sensation of whirling in the head. Unlike with light-headedness, when someone is dizzy, he or she will have a tendency to fall down.

otolithic membranes of the utricle maculae lag behind, bending the stereocilia backward. In contrast, when you stop moving, the otolithic membranes slide forward, bending the hairs in that direction. Similarly, when you are in an elevator that moves up, the otolithic membranes of the saccule briefly lag behind and pull down on the stereocilia. When the elevator stops, the membranes keep moving for an instant, bending the hairs upward. Thus, inertia of the membranes is especially important in detecting linear acceleration (or deceleration); the utricle senses horizontal movement, whereas the saccule responds to vertical acceleration.

When stereocilia bend toward a kinocilium, the hair cell depolarizes and releases more neurotransmitter. As a result, a larger number of signals are sent to the brain. In contrast, when stereocilia bend away from a kinocilium, the receptor hyperpolarizes and releases less neurotransmitter. It is important to note that the maculae only respond to changes in acceleration or velocity of the head. These receptors also adapt quickly, so they do not provide input when the position of the head does not change.

THE SEMICIRCULAR DUCTS

Rotational acceleration is detected by the three semicircular ducts, each of which is housed in a bony **semicircular canal** of the temporal bone. The anterior and posterior semicircular ducts are positioned vertically, at right angles to each other. The lateral duct is about 30° from the horizontal plane. The location of the three canals allows a different duct to be stimulated by rotation of the head in different planes, e.g., when we shake our head from side to side to say "no," nod it up and down to indicate "yes," or tilt it from shoulder to shoulder.

Each semicircular duct opens into the utricle and has a swollen sac at one end called the **ampulla**, which is an expanded region that contains sensory cells. Within each ampulla is a mound of hair cells and supporting cells known

as the **crista ampullaris** (or simply *crista*). The stereocilia and kinocilium are embedded in a gelatinous region called the **cupula**, which extends from a crista to the roof of the ampulla. Like the maculae, the cristae are stimulated by head movements, but, in this case, rotational (angular) movements stimulate them most.

ACTIVATION OF CRISTAE RECEPTORS

The cristae respond to changes in the velocity of angular or rotational movements of the head. When our head turns, the semicircular ducts, which contain endolymph, rotate as well. However, the endolymph lags behind for an instant, thereby pushing the cupula and bending the stereocilia. This, in turn, stimulates the hair cells to change their membrane potential. As with maculae receptors, bending stereocilia toward the kinocilium leads to a depolarization, whereas movement in the

YOUR HEALTH: Motion Sickness

A common equilibrium disorder is motion sickness. It appears to be caused by a mismatch of sensory input to the brain. For instance, when you read in a moving car, the visual inputs tell your brain that the body is fixed with reference to a stationary environment (the book). However, as the car makes turns and changes speed, the vestibular apparatus detects movement and sends impulses that contradict the visual information. Apparently, when the brain gets this kind of conflicting information, it somehow causes the symptoms of motion sickness. These include excessive salivation, turning pale, rapid deep breathing, profuse sweating, nausea, and vomiting. Similarly, when you are in a cabin on a boat, the visual inputs suggest that your body is not moving, but the inner ear can sense the ship moving in the water. This leads to seasickness, which is a form of motion sickness. Over-the-counter anti-motion drugs can relieve this condition by inhibiting vestibular inputs to the brain.

other direction causes a hyperpolarization of hair cells. Because the axes of the hair cells in complementary ducts are opposite, rotation in a particular direction causes the receptors in one ampulla of the pair to depolarize and the receptors in the other to hyperpolarize. However, after about 25 to 30 seconds of continual rotation, the endolymph catches up with the movement of the ducts and stimulation of hair cells ceases. This explains why, when we are blindfolded, we often cannot tell whether we are moving at a constant speed or not moving at all after the first few seconds of rotation.

CONNECTIONS

The sense of equilibrium allows us to detect the position of our head in space by monitoring gravity, linear acceleration, and rotation. The receptors for equilibrium are found in the vestibular apparatus of the inner ear, which consists of three semicircular canals and two chambers: the anterior saccule and the posterior utricle. The semicircular canals provide information about rotational movements of the head, which is referred to as dynamic equilibrium. The saccule and utricle give the brain information about your position in space with respect to gravity, called static equilibrium.

The sensory receptors for static equilibrium are patches of hair cells (2 by 3 mm), called the macula sacculi and the macula utriculi, that respond to linear acceleration forces but not to rotation. Each macula is a flat epithelial patch that contains supporting cells and scattered receptors cells (hair cells). Each hair cell has stereocilia and a true cilium called the kinocilium. The tips of the stereocilia and kinocilium are embedded in a gelatinous otolithic membrane, which is studded with tiny calcium carbonate crystals called otoliths. When the head tilts, the weight of the otolithic membrane bends the stereocilia, thereby stimulating the hair cells. The brain interprets head orientation by comparing vestibular inputs to each other and to other inputs from the eyes and stretch receptors.

Rotational acceleration is detected by the three semicircular ducts, each housed in a semicircular canal of the temporal bone. The anterior and posterior semicircular ducts are positioned at right angles to each other; the lateral duct is about 30° from the horizontal plane. The semicircular ducts are filled with endolymph and contain a swollen sac at one end called the ampulla. Within each ampulla is a mound of hair cells and supporting cells known as the crista ampullaris. The stereocilia and kinocilium are embedded in a gelatinous region called the cupula, which extends from a crista to the roof of the ampulla.

The cristae respond to changes in the velocity of angular or rotational movements of the head. However, the endolymph lags behind for an instant, thereby pushing the cupula and bending the stereocilia. This, in turn, stimulates the hair cells. After about 25 to 30 seconds of continual rotation, the endolymph catches up with the movement of the ducts and stimulation of the hair cells stops.

10

Sense of Thirst and Hunger

The feelings of thirst and hunger are not connected to a particular sense organ like the senses of vision or hearing are. Instead, they are triggered by one or more stimuli that come from inside the body itself. For these reasons, they are often referred to as part of the general sensations. Stimuli that are strong enough to elicit general sensations also cause physiological and behavioral changes that try to reduce the intensity of such sensations. That is, stimuli for general sensations induce **drives**—motivational states that influence us to try to get whatever the body feels we lack. For instance, a lack of water in the body not only leads to a sensation of **thirst**—the desire for fluid, especially water—but it also encourages us to search for something to drink. Thus, drives associated with general sensations help us survive.

WATER BALANCE

The human adult body is 70 to 75% water by weight, without taking fat deposits into account. Amazingly, healthy people have an incredible ability to maintain the concentration of their body fluids within very narrow limits. In fact, body water normally increases or decreases about 0.22% of the body weight. For example, in a 70-kg (154-lb) man, a typical variation of body water is only around 150 milliliters out of about 40 liters (42.3 qts) of total body water.

In order to remain properly hydrated, our water intake must equal our water output. Water output occurs by several routes, most

of which are obligatory, meaning they cannot be prevented (Figure 10.1). For instance, some water loss occurs as water leaves directly through our skin. Obligatory water also leaves the body in the form of vapor every time we exhale. Water output through our skin and from breathing is often called **insensible water loss** because we do not consciously notice it. Additional obligatory water loss occurs when we perspire, urinate, and defecate.

The amount of water intake varies quite a bit from person to person and is influenced by personal habit as well as thirst. However, it is typically around 2.5 liters (2.6 quarts) per day in adults. Most of this water enters our body through liquids we drink. We get extra water from solid foods (there is a lot of water in many fruits and vegetables), and some water is actually produced in our bodies through cellular metabolism (this is called **metabolic water**).

REGULATION OF WATER INTAKE

Fluid intake is governed by the sensation of thirst. Unfortunately, the regulation of this sense is poorly understood. Evidence indicates that dehydration causes blood volume and pressure to drop, while blood osmolality, or the amount of particles in the blood, rises. Some of these physical changes are detected by the **thirst center** of the hypothalamus, which contains osmoreceptors. Typically, when someone loses more water than 0.5% of the body weight (about 350 ml for a 70-kg person), has a 10% reduction in plasma volume, or an increase of 1 to 2% in plasma osmolality, it will be enough to cause a dry mouth and stimulate the thirst center. A dry mouth occurs as a direct result of an increase in plasma osmolality, since this condition inhibits fluid flow from blood vessels. Because the salivary glands get water from the blood, less saliva is produced when we are dehydrated. However, it is not certain whether our primary motivation to drink is simply a dry mouth. Studies show that people who do not secrete saliva and experimental animals that have

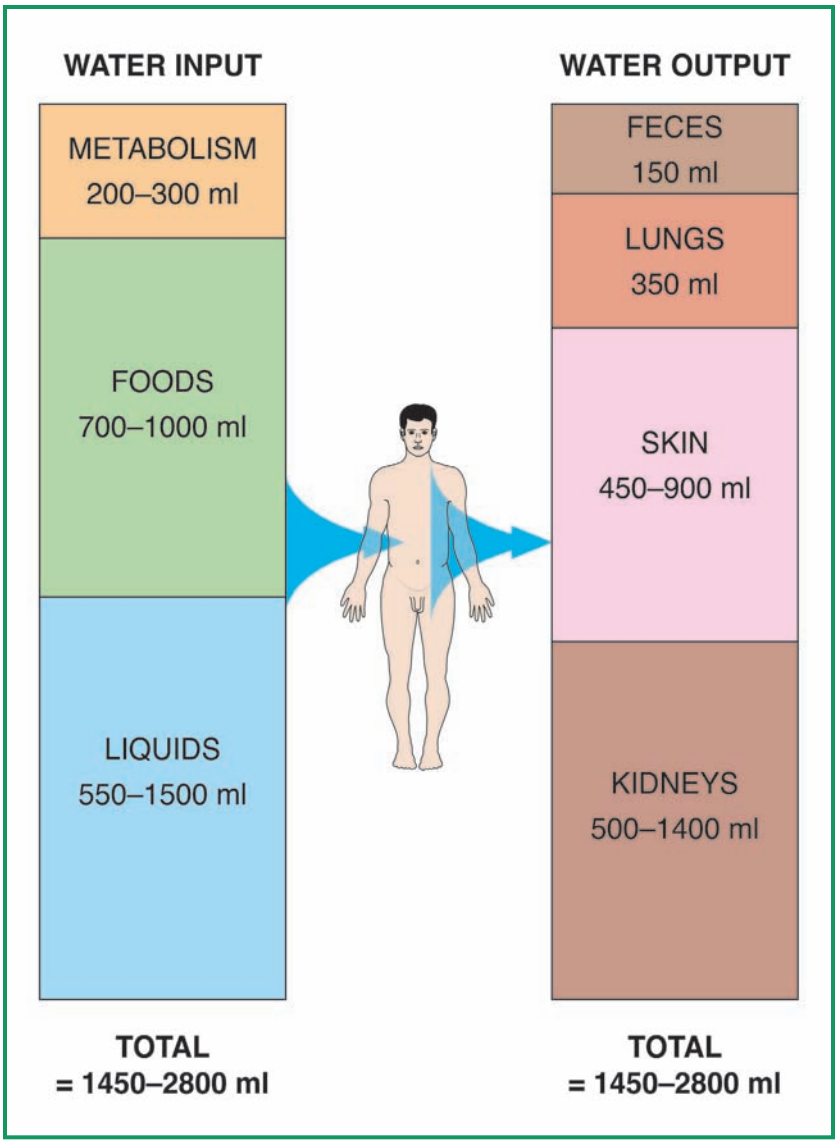

Figure 10.1 The body has a thirst mechanism to balance water intake and output. The body loses water through urination, defecation, and sweating, and through the skin and lungs. How much water we take in must equal how much water we lose. The body is amazingly efficient at balancing the amount of water we take in with the amount we lose, as seen here.

had their salivary ducts tied off do not drink any more than normal individuals do (except when they eat because they need water to moisten food).

The hypothalamic thirst center is stimulated when its osmoreceptor cells lose water when the water leaks through cells to the extracellular fluid. This loss of water causes the cells to depolarize, which presumably leads to a sensation of thirst, thereby motivating us to drink. The thirst center also responds to angiotensin II, a hormone produced when our blood pressure falls. **Antidiuretic hormone** (ADH) is a hormone released by the pituitary gland in response to rising plasma osmolality (the amount of particles in the blood plasma). It, too, can activate hypothalamic osmoreceptor cells. Long-term quenching of thirst depends on absorbing water from the small intestine, a process that lowers the osmolality of plasma. This, in turn, inhibits the thirst center and also causes saliva to form. However, it takes approximately 30 minutes for this process to take effect after we drink water. Obviously, it would be impractical if we had to drink for this length of time in order to feel satisfied. Fortunately, there are also short-term mechanisms that act more quickly to quench thirst.

Short-term thirst quenching occurs almost as soon as we begin to drink water, even though we have not had enough time to absorb this water into the bloodstream. It appears that simply moistening and cooling the membranes of the mouth and throat reduces the sensation of thirst. For instance, laboratory rats will drink less when their water is cool compared to when it is warm. In addition, moistening a rat's mouth temporarily satisfies thirst even if this water is drained from the esophagus before it reaches the stomach. Thirst is further satisfied when stretch receptors in the stomach and small intestine are stimulated, since these receptors send signals to the thirst center. This theory has been tested by allowing dogs to drink and then draining the water from the esophagus while the stomach is inflated with a balloon.

Scientists believe that the "premature" dampening mechanisms of thirst described above keep us from drinking more than we need to and overdiluting our body fluids. However, these short-term mechanisms are only effective for about 30 to 45 minutes. In other words, if we do not actually get sufficient water into the bloodstream, the sensation of thirst soon returns. Only a drop in blood osmolality produces a long-lasting effect of thirst quenching.

REGULATION OF WATER OUTPUT

We cannot avoid losing certain amounts of water. This helps explain why we cannot survive for long without drinking (because fluid deficiency occurs when output exceeds intake over a long enough period of time). The only way to control water output significantly is though variations in urine volume. Although the kidneys are well adapted to eliminate excess water, they cannot prevent water loss. That is, humans have to flush some substances out of the body with water. The kidneys also are not capable of replacing lost water. As a result, the kidneys do not restore fluid volume during dehydration, but merely slow the rate of water loss until more water is ingested to restore balance.

The solute concentration (amount of substances dissolved) and volume of urine can vary quite a bit and depend on several

YOUR HEALTH: Thirst

The sensation of thirst is an effective mechanism. However, it does not always reliably tell us how much water we need. For instance, during athletic events, we can satisfy our thirst by just drinking enough to cool our mouths and make them less dry. But that does not mean we have drunk enough liquids to restore body fluid balance. In addition, elderly people may not recognize or pay attention to thirst signals. In contrast, some kidney or heart patients who are "fluid-overloaded" by intravenous injection may still feel thirsty.

factors, such as the amount of fluid intake, diet, and water loss by other means, such as perspiration. Normally, the kidneys begin to get rid of excess water about 30 minutes after it has been ingested, with most elimination taking place after about 60 minutes. This delay reflects the amount of time it takes for water to be absorbed from the small intestine into the blood and to inhibit the release of antidiuretic hormone (ADH) from the pituitary gland, which causes the kidneys to produce a less concentrated, but more plentiful, urine. Conversely, if blood volume or pressure is too low, ADH release is stimulated, and urine output decreases in volume (Figure 10.2).

YOUR HEALTH: Diabetes

When not enough ADH is secreted, it results in a disease called diabetes insipidus, which causes a person to let out huge amounts of urine and suffer from intense thirst. *Diabetes* is a term that refers to "overflow" and *insipidus* means "tasteless." This disorder can be caused by a head injury that damages the hypothalamus or pituitary gland. Although it is certainly inconvenient, it is not usually life-threatening, as long as the thirst center works normally and the person drinks enough water to prevent dehydration. However, diabetes insipidus can be fatal if the patient is unconscious or in a coma and does not get enough fluids. This is why doctors carefully monitor the urine flow of accident victims who have head trauma.

Diabetes insipidus differs from the disease diabetes mellitus, which also causes a large amount of urine output and thirst, but is caused instead when insulin is not released or used properly by the body. Unlike in people who have diabetes insipidus, the urine of individuals with diabetes mellitus also contains glucose (*mel* means "honey"). These two disorders got their names from the way they were first diagnosed. In other words, at one time, health-care providers tasted patients' urine to figure out what was causing the excessive urine output.

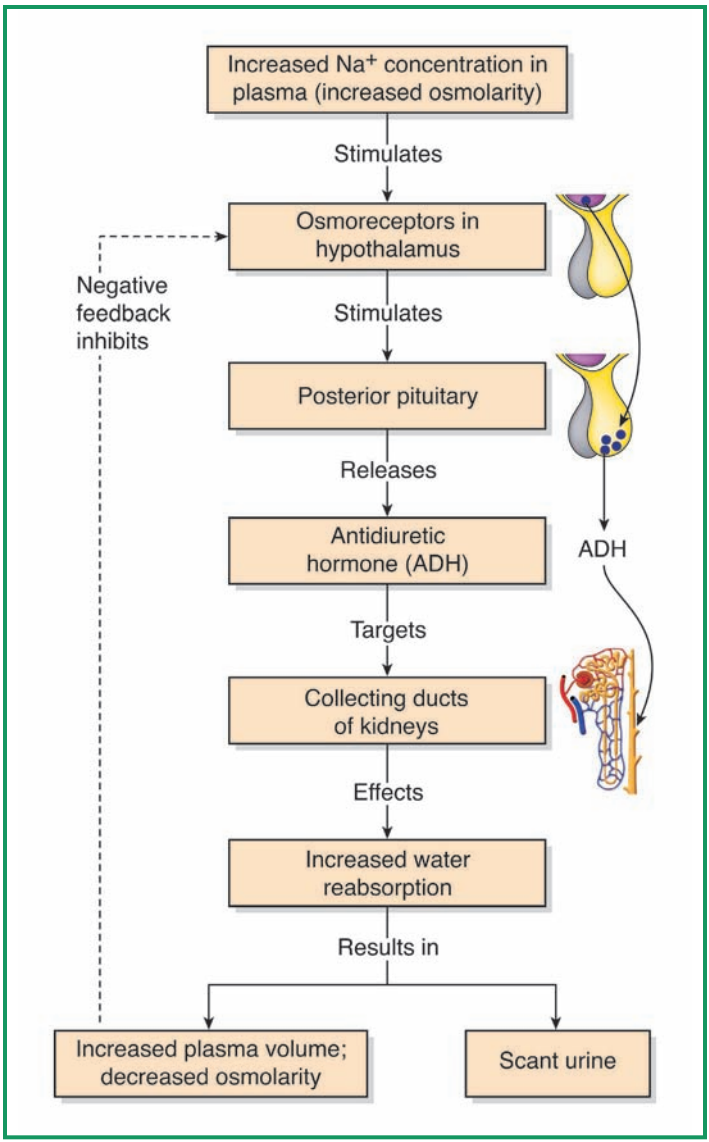

Figure 10.2 Antidiuretic hormone (ADH) helps conserve body water when we need it to make up for too much fluid output. Osmoreceptors of the hypothalamus monitor the concentration of chemicals in body fluids and trigger or inhibit the release of ADH as needed. Releasing ADH leads the kidneys to reabsorb water, which reduces the amount of urine expelled.

DISORDERS OF WATER BALANCE

Fluid deficiency occurs when water loss exceeds water intake over a long enough period of time. There are two kinds of deficiencies—volume depletion and dehydration—which differ in the relative loss of water and electrolytes, and the resulting osmolality of the extracellular fluid.

Volume depletion occurs when proportionate amounts of water and electrolytes (mostly sodium chloride) are lost without being replaced. This can happen with excessive bleeding, severe burns, or chronic diarrhea and vomiting. In this case, the volume of total body water declines, but the osmolarity of body fluids remain normal. In contrast, **dehydration** (negative water balance) occurs when the body loses a lot more water than electrolytes, so the osmolarity of extracellular fluids increases. The most common cause of dehydration is a lack of drinking water—for instance, when someone is stranded at sea or in a desert. It also can be caused by an overuse of diuretics (agents that cause you to urinate), endocrine disorders (such as diabetes mellitus and diabetes insipidus), and prolonged exposure to cold weather. A serious consequence of severe dehydration is that the blood does not have a high enough plasma volume to circulate normally. This can lead to **hypovolemic shock**, a life-threatening condition in which the heart is unable to supply enough blood to the body.

It is also possible to have too much body fluid. However, this is not very common because when the osmolality of the extracellular fluid drops, ADH release is inhibited, which allows the kidneys to make up for excessive water intake by excreting more urine. Nonetheless, kidney failure or drinking far too much water in a short time period can cause excess fluid retention, or **hypotonic hydration** (also called water intoxication). This makes water leak into tissue cells, making them swell as they become abnormally hydrated. Water intoxication is particularly damaging to neurons. If not treated, it can quickly lead to disorientation, convulsions, coma, and death.

It also causes excess fluid to accumulate in the lungs, which inhibits gas exchange. Water intoxication can be treated by intravenous injection with mannitol—a special carbohydrate that increases the osmolality of the extracellular fluid and helps draw water out of cells.

Fluid may also accumulate abnormally in a particular location. In such a case, the total body water may be normal, but the volume of circulating blood may drop so low that the circulatory system may collapse. The most common abnormal accumulation of fluid is called **edema**, in which fluid gathers in the interstitial spaces (spaces between cells), causing tissue to swell. This can be caused by increased blood pressure, localized blood blockage, congestive heart failure, or high blood volume. It also can occur when the capillaries let too much fluid pass through them, such as during an inflammatory response (e.g., an allergy to a bee sting).

YOUR HEALTH: Cold Weather

Profuse sweating in hot weather is an obvious threat to fluid balance. However, physiological changes associated with cold weather can also cause fluid balance problems. When the body is very cold, it reduces heat loss by constricting blood vessels and tissues under the skin. This, in turn, raises blood pressure, which slows the release of antidiuretic hormone and releases more atrial natriuretic peptide (a hormone the heart secretes in response to increased blood volume or pressure). Together, these changes lead to an increase in urine output. In addition, cold air is relatively dry (it holds less moisture than warm air), which makes the body lose more water through breathing. As a result, prolonged exposure to cold weather can result in sufficient water loss to cause hypovolemia, a decrease in the volume of circulating blood. This helps explain why it is important to drink plenty of fluids when you take part in winter sports and other cold weather activities, such as shoveling snow.

SENSE OF HUNGER

A person is said to be in energy balance if his or her energy content (calories) from food equals the amount of energy used to do muscular work, and for the processes of metabolism and heat loss. Excess food intake causes fat to be deposited, thereby increasing body weight. In contrast, a lack of food makes the body use fat deposits to do work. If this goes on for a long time, it can impair body function and eventually lead to death. We have the ability to adapt our food intake to changing needs, depending on the amount of physical activity, climate, and the nutritional value of the food we eat. In fact, the body weight of most people is amazingly stable because our bodies have ways to control food intake.

Hunger is a general sensation resulting from a lack of food, usually accompanied by the desire to eat. Like the sensation of thirst, its physiological mechanisms are not well understood. As we all know from experience, hunger comes on when the stomach is empty, and vanishes once the stomach is filled with food. It, therefore, seems apparent that hunger is stimulated, at least in part, by stomach peristalsis (**hunger contractions**), which occur in a mild form soon after the stomach empties. These contractions get more intense over a period of hours, and they give us a powerful incentive to eat. However, other factors also influence appetite in ways similar to the mechanism of thirst. For instance, just chewing and swallowing food briefly satisfies appetite, even if the food is removed from the esophagus before it reaches the stomach. In addition, inflating the stomach with a balloon inhibits hunger, even if an animal has not actually swallowed any food.

As with thirst, the hypothalamus is involved with hunger feelings and satiety (a feeling of fullness or satisfaction). The **feeding center** of the hypothalamus is important for providing hunger sensations. For instance, when this part of the brain is destroyed in laboratory rats, they exhibit a loss of appetite and will starve to death if not force-fed. In contrast, damage to

the **satiety center** causes extreme overeating (**hyperphagia**), leading to **obesity**. It has been shown that the satiety center has **glucostats**—neurons that rapidly absorb blood glucose after a meal. Evidence indicates that when this occurs, the glucostats send inhibitory signals to the feeding center, thereby suppressing appetite (this has been termed the **glucostat hypothesis** of hunger). Some weight-loss drugs work by inhibiting the feeding center. As blood glucose levels drop between meals, inhibitory signals from the satiety center decline, allowing the feeding center to become more active, causing the sense of hunger to return.

A number of hormones also play a role in appetite regulation and feeding behavior. For instance, the hypothalamus produces a hormone called **neuropeptide Y**, which leads us to crave carbohydrates and is a potent appetite stimulant. In contrast, the presence of amino acids and fatty acids in the small intestine stimulate cells to secrete a hormone called **cholecystokinin** (**CCK**), which acts as an appetite suppressant. Other chemicals produced in the body make us feel full and satisfied.

Interestingly, adipose cells (fat cells) can release a hormone called **leptin**, which circulates at levels related to the body's fat reserves. In fact, leptin levels are thought to serve as an indicator of the body's total energy stores and provide a way for the body to control hunger and long-term caloric intake. In addition, a number of studies indicate that the overall satiety signal is leptin, which is secreted over a period of hours exclusively by fat tissue in response to an increase in fatty mass in the body. Leptin acts on the hypothalamus and inhibits the secretion of neuropeptide Y, thereby suppressing appetite.

As previously noted, scientists do not understand completely how the sense of hunger works. Most present-day studies are trying to determine the roles played by neural signals from the digestive tract, blood-borne signals related to body energy stores, hormones, body temperature (increased body temperature may inhibit eating), and psychological

factors. Keep in mind that these mechanisms are not mutually exclusive, and most of these factors seem to operate through feedback signals to the feeding and satiety centers of the brain.

CONNECTIONS

The feelings of thirst and hunger are not tied to a particular sense organ as the senses of vision and hearing are. As a result, they are often referred to as part of the general sensations. The human adult body consists of 70 to 75% water by weight. In order to remain properly hydrated, our water intake must equal our water output. Water output occurs through several routes, most of which are obligatory. Insensible water loss is one type of obligatory output, which occurs through our skin and when we breathe. Obligatory water output also occurs when we perspire, urinate, and defecate. Most of this water enters our body through ingested liquids. Additional water is obtained from solid foods, and some water is actually produced in our bodies by cellular metabolism (called metabolic water).

Fluid intake is governed mainly by the sensation of thirst. Dehydration causes a reduction in blood volume and pressure,

YOUR HEALTH: BMI

Obesity is defined as a body weight of more than 20% above what doctors recommend for a person's age, gender, and height. The National Institutes of Health (NIH) estimate that 50% of the people living in the United States today are overweight and 33% are clinically obese. The official measure of body weight is called the body mass index (BMI), an index of a person's weight relative to height. To estimate your BMI, multiply your weight in pounds by 705 and then divide by the square of your height in inches. A BMI of 20 to 25 is considered optimal for most people; a BMI over 27 is considered overweight and above 30 is considered obese.

while also raising blood osmolality. Some of these changes are detected by the thirst center of the hypothalamus. The thirst center is stimulated when its osmoreceptor cells lose water through osmosis, which leads to a sensation of thirst that motivates us to drink.

The only way to control water output significantly is though variations in urine volume. Although the kidneys are well adapted to eliminate excess water, they cannot prevent water loss. Consequently, the kidneys do not restore fluid volume during dehydration, but instead slow the rate of water loss until more is ingested to restore balance. The solute concentration and volume of urine depends on several factors, including the amount of fluid intake, diet, and water loss by other avenues, such as perspiration.

Fluid deficiency occurs when water loss exceeds water intake over a sufficient period of time. Volume depletion occurs when proportionate amounts of water and electrolytes are lost without replacement. In contrast, dehydration (negative water balance) occurs when the body loses significantly more water than electrolytes, increasing the osmolality of extracellular fluids. The most common cause of dehydration is a lack of drinking water, but it can also be caused by the overuse of diuretics, by endocrine disorders, and by prolonged exposure to cold weather.

It is possible to suffer from fluid excess. For instance, renal failure or drinking extraordinary amounts of water in a short time period can lead to excess fluid retention or hypotonic hydration. This condition promotes net osmosis of water into tissue cells, causing them to swell as they become abnormally hydrated.

Fluid may also accumulate abnormally in a particular location. The most common form is called edema, which is the abnormal accumulation of fluid in the interstitial spaces, causing swelling of a tissue.

A person's energy balance is maintained in equilibrium if the energy content (calories) of food equals the energy used for

muscular work, metabolism, and heat loss. Physiological mechanisms control food intake. Lack of food causes the sensation of hunger, and subsequent food intake leads to satiety.

Hunger is a general sensation projected to the stomach region and is stimulated partly by stomach peristalsis (hunger contractions). As with thirst, the hypothalamus is involved with hunger sensations and satiety. The feeding center is important in providing hunger sensations and the satiety center provides signals that let us know we are full. The satiety center has neurons called glucostats that send inhibitory signals to the feeding center, thereby suppressing appetite (glucostat hypothesis of hunger).

A number of hormones also play a role in appetite regulation and influence feeding behavior. Neuropeptide Y causes us to crave carbohydrates. In contrast, the hormone cholecystokinin (CCK) acts as an appetite suppressant. Adipose (fat) cells can release a hormone called leptin, which circulates at levels related to the body's fat reserves, and appears to be the overall satiety signal.

Accommodation The ability of the lens of the eye to change its shape in order to keep the focal length constant.

Action potential All-or-none electrical signal that is conducted along nerve axons.

Adaptation A decrease in the responsiveness of receptors during continued stimulation.

Adenylate cyclase Enzyme that converts ATP to cyclic AMP (cAMP).

Ageusia A condition in which individuals experience no sensation of taste.

Amplitude The height of periodic waves, such as sound waves.

Ampulla A swollen sac at one end of a semicircular duct that contains sensory cells.

Amygdala A structure in the brain; part of the limbic system that labels information to be remembered.

Analgesics Drugs that act as painkillers.

Anosmia A condition in which a specific odor or odors cannot be detected.

Anterior cavity A smaller cavity in front of the lens of the eye filled with aqueous humor.

Anterior chamber Part of the anterior cavity of the eye located between the cornea and the iris.

Antidiuretic hormone (**ADH**) Also known as vasopressin; a chemical secreted by the pituitary gland that raises blood pressure and reduces the flow of urine.

Aqueous humor A transparent fluid that fills the anterior and posterior chambers of the eye.

Astigmatism A defect in vision due to abnormal curvature of the cornea or lens.

Auditory tube Passageway extending from the middle ear to the pharynx; the Eustachian tube.

Auricle Portion of the outer ear composed of elastic cartilage covered with skin.

Autonomic Occurring involuntarily.

Glossary

Axon Long, narrow part of a neuron (nerve cell) that conducts electrical signals called action potentials.

Baroreceptor Receptor that responds to changes in pressure.

Basal cell Cell of a taste bud that actively divides and differentiates into new supporting cells and sensory cells.

Basilar membrane Membrane that separates the scala media from the scala tympani in the inner ear.

Bipolar cells Cells in the retina that help perform preliminary processing and integration of visual information.

Blind spot Area in the retina that lacks photoreceptors; the place where the optic nerve exits the eye.

Blue cone Photoreceptor whose pigment responds maximally to wavelengths of light around 420 nm.

Body mass index (**BMI**) Measure of body weight relative to a person's height.

Bony labyrinth A maze of passageways in the temporal bone of the ear containing the vestibule, the cochlea, and the semicircular canals.

Canal of Schlemm Opening at the junction of the sclera and cornea of the eye that drains aqueous humor from the anterior chamber.

Cataract A disease of the eye characterized by clouding of the lens.

Cerebral cortex Integrating center in the brain for higher functions such as reasoning, speech, language, and imagination.

Cerumen Soft, yellow-brown secretion found in the external ear canal; also called earwax.

Ceruminous gland Modified sweat gland in the auditory canal.

Chemoreceptor Receptor cell that responds to chemicals in solution.

Cholecystokinin (**CCK**) Hormone secreted by the small intestine that acts as an appetite suppressant.

Choroid Highly vascular, deeply pigmented membrane of the tunica vasculosa.

Ciliary body Thickened part of the tunica vasculosa that consists of interlacing smooth muscle bundles, which are important for controlling the lens shape.

Circumvallate papillae Largest of the lingual papillae; arranged in the shape of the letter "V" at the back of the tongue.

***cis*-retinal** Bent form of retinal when it is bound to opsin.

Cochlea A winding, snail-shaped tube of the bony labyrinth of the inner ear that contains the receptors for hearing.

Color blind Having a defect in vision due to a sex-linked hereditary lack of one or more of the cone types.

Complex receptor Localized collections of cells associated with the special sense organs.

Conchae The three scroll-like ridges that project from the wall of the nasal cavity.

Conduction deafness Loss of hearing due to a hindrance of sound conduction to the fluids of the inner ear.

Cone Photoreceptor that operates in bright light and provides high-acuity color vision.

Conjunctiva An epithelium that covers the inner surface of the eyelids and the outer surface of the eye.

Conjunctivitis Inflammation of the conjunctiva resulting from irritation or infection.

Convex Evenly curved to resemble a segment of a sphere.

Cornea Transparent anterior portion of the tunica fibrosa of the eye.

Crista ampullaris Mound of hair cells and supporting cells within each ampulla of a semicircular duct; also called crista.

Cupula Gelatinous region in a semicircular duct that extends from a crista to the roof of the ampulla.

Cyclic adenosine monoposphate (**cAMP**) An intracellular messenger formed from ATP by the action of adenylate cyclase.

Dark adaptation Changes that occur in light-adapted eyes in order for vision to occur in dim light.

Deafness Any loss of hearing, regardless of cause.

Decibel (**dB**) Unit for expressing the loudness of sound.

Dehydration When the body loses significantly more water than electrolytes, so the osmolality of extracellular fluids increases.

Dendrite Threadlike extension of a neuron (nerve cell) that conducts the nerve impulse toward the cell body.

Dermal papillae Protuberances on the skin that extend into the epidermal layer and contain the corpuscles involved in the sense of touch.

Diabetes insipidus Diabetes characterized by excessive urination and thirst caused by inadequate secretion of antidiuretic hormone (ADH).

Diabetes mellitus Diabetes resulting from inadequate production or utilization of insulin.

Diplopia Double vision.

Drives Motivational states that influence us to provide or obtain whatever the body feels is lacking.

Dynamic equilibrium Sensory information about rotational movements of the head.

Dysgeusia A condition in which individuals experience a distortion of taste.

Edema Abnormal accumulation of fluid in the interstitial spaces, causing swelling of tissues.

Electromagnetic energy A form of energy that travels in space as waves and can be measured in photons.

Electromagnetic spectrum The entire range of wavelengths or frequencies of electromagnetic energy.

Emmetropia Condition in the eye when parallel rays are focused precisely on the retina, making vision perfect.

Encapsulated nerve endings One or more fiber terminals of sensory nerves enclosed in a connective tissue capsule.

Endolymph Fluid within the membranous labyrinth of the inner ear.

Equilibrium State of balance.

External auditory canal Passageway leading from the outer ear to the eardrum.

Exteroceptor Receptor that responds to stimuli arising outside the body.

Extrinsic eye muscle Muscle attached directly to the external surface of the eyeball and the wall of the orbit.

Eyebrow Short, coarse hairs that overlie the supraorbital margins of the skull.

Eyelid Movable fold of skin over the eye.

Fast pain An initial feeling of sharp, localized, stabbing pain perceived at the time of an injury.

Feeding center Region in the hypothalamus that leads to the sensation of hunger when stimulated.

Fight-or-flight response A reaction in which the body becomes alarmed when confronted by an external stimulus and prepares either to defend itself against the source of the stimulation or to run away from the perceived threat.

Filiform papillae Tiny bumps that cover the surface of the tongue that lack taste buds.

Focal distance Distance between the center of a lens and its focal point.

Focal point A single spot on the retina where focused light rays converge.

Foliate papillae Folds along the back edges of the tongue that are well developed in children but less prominent and numerous in adults.

Fovea centralis Location in the retina that contains only cones, used for most acute vision.

Frequency The number of waves that pass a given point over a period of time.

Fungiform papillae Mushroom-shaped structures scattered over the entire surface of the tongue.

Ganglion cells Cells in the retina that generate action potentials.

General sense Sense that includes tactile sensation (touch, pressure, stretch, or vibration), temperature monitoring (heat and cold), and pain.

Glands of Zeis Small sebaceous glands associated with eyelash follicles.

Glaucoma Disease of the eye characterized by an increase in intraocular pressure resulting from reduced drainage of aqueous humor.

Glomeruli Complex spherical structures in the olfactory bulb.

Glucostat Neuron in the satiety center that absorbs glucose after a meal.

Glucostat hypothesis The idea that glucostats send inhibitory signals to the feeding center after a meal, thereby suppressing appetite.

Golgi tendon organ Proprioceptor located in tendons that monitors tension produced during muscular contraction.

Granule cell Cell of the olfactory bulb that inhibits the activity of mitral cells.

Green cone Photoreceptor whose pigment responds maximally to wavelengths of light around 530 nm.

Gustation The sense of taste.

Gustatory cell Receptor cell for taste.

Hair cell Epithelial cell of the organ of Corti that is topped with stereocilia.

Hertz (**Hz**) Number of cycles of a wave per second.

Hunger Sensation resulting from a lack of food, usually accompanied by the desire to eat.

Hunger contraction Muscular contraction in the normal empty stomach.

Hyperopia Defect in vision in which light rays come to a focus behind the retina; farsightedness.

Hyperphagia Extreme overeating, which leads to obesity.

Hypogeusia Condition where the threshold (minimum concentration) for taste perception is above the normal range, making it harder to taste substances.

Hypothalamus Major control center in the brain for the body's autonomic functions.

Hypotonic hydration Excess fluid retention that can be caused by kidney failure or drinking an extraordinary amount of water in a short time period.

Hypovolemic shock Condition in which rapid fluid loss causes multiple organ failure.

Incus Middle ear bone resembling an anvil in shape.

Inferior meatus A horizontal passageway along the lateral wall of the nasal cavity.

Inner ear The bony labyrinth and a series of fluid-filled membranous sacs and ducts contained within it (membranous labyrinth).

Inner hair cell Receptor cell for hearing; converts sound energy into electrical signals.

Inner segment Region of a photoreceptor that corresponds to the cell body of a nerve cell.

Insensible water loss Water loss through the skin and from breathing that is not usually noticed.

Interoceptor Receptor that detects stimuli arising within the body, such as those from the internal organs and blood vessels.

Iris Visible colored part of the eye suspended between the cornea and the lens.

Ischemia Deficient blood flow to a specific body region or part.

Kinocilium A true cilium on the surface of hair cells.

Krause end bulb Receptor for touch located in mucous membranes.

Labeled line code Nerve tracts that deliver sensory information to specific regions of the brain.

Lacrimal apparatus Structures responsible for the production, distribution, and removal of tears.

Lacrimal canal Tiny tubes that connect the lacrimal puncta to the lacrimal sac.

Lacrimal caruncle Soft tissue mass that contains sebaceous and sweat glands, located on the conjunctiva near the medial commissure.

Lacrimal gland Structure that secretes tears.

Lacrimal puncta Tiny openings that drain tears from the eye.

Lacrimal sac Upper dilated portion of the nasolacrimal duct.

Lacrimal secretion A dilute saline solution; tears.

Lateral commissures Where the two eyelids meet at the lateral side of the eye.

Lens Transparent, flexible structure that can change its shape to allow for precise focusing of light on the retina.

Leptin Hormone released by fat cells that acts on the hypothalamus and inhibits the secretion of neuropeptide Y, thereby suppressing appetite.

Light adaptation Changes that occur in dark-adapted eyes in order for vision to occur in bright light.

Limbic system Part of the brain, including the amygdala and hypothalamus, that plays an important role in feeling emotions.

Lingual papillae Peg-like projections that give the tongue a slightly rough feel.

Lobule The earlobe.

Loudness The perception of sound energy; the pressure difference between the compressed and rarefied areas.

Lysozyme An enzyme found in tears that has antibacterial properties.

Maculae Anatomical structures that take the form of "spots" that differentiate them from the surrounding structures.

Macula lutea Retinal region that contains mostly cones.

Macula sacculi Sensory receptor for static equilibrium situated nearly vertically in the wall of the saccule.

Macula utriculi Sensory receptor for static equilibrium situated nearly horizontally on the floor of the utricle.

Malleus Middle ear bone resembling the shape of a hammer, attached to the eardrum.

Mechanoreceptor Receptor cell that responds to physical deformation caused by touch, pressure, stretch, tension, or vibration.

Medial commissure Where the two eyelids meet near the bridge of the nose.

Meibomian gland One of the sebaceous glands between the tarsi and conjunctiva of eyelids.

Meissner's corpuscle Phasic receptor in the skin that senses light touch and texture.

Membranous labyrinth Series of fluid-filled membranous sacs and ducts contained within the bony labyrinth.

Merkel disk Tonic receptor in the skin that senses light touch.

Metabolic water Water produced in the body through cellular metabolism.

Middle ear Small, air-filled space located in the tympanic cavity of the temporal bone.

Mitral cell Second-order neuron that transmits impulses from an olfactory bulb to destinations within the brain via the olfactory tracts.

Modality Type of sensation a stimulus produces.

Motion sickness An equilibrium disorder leading to symptoms of sweating, pallor, nausea, and vomiting.

Muscle spindle Proprioceptor found throughout skeletal muscles that responds to muscle stretch.

Myelin sheath Insulating layer that is composed of Schwann cells and surrounds nerve axons.

Myopia Defect in vision in which light rays come to a focus in front of the retina; nearsightedness.

Nasal cavity Space between the roof of the mouth and the floor of the skull.

Nasal septum The partition dividing the nasal cavity into two spaces, left and right.

Nasolacrimal duct Duct that drains tears from the lacrimal sac to the nasal cavity.

Neuron Nerve cell; capable of conducting electrical signals.

Neuropeptide Y Hypothalamic hormone that acts as a potent appetite stimulant.

Night blindness Inability to see well in dim light or in darkness; defect in vision due to a lack of rhodopsin in the rods.

Nociceptor Receptor that responds to potentially damaging stimuli and causes pain.

Obesity A condition in which an individual is extremely overweight.

Olfaction The sense of smell.

Olfactory bulb The distal end of the olfactory tract, which is composed mainly of mitral cell axons.

Olfactory cell Receptor cell for the sense of smell.

Olfactory cilia Microvilli on the surface of olfactory cells.

Olfactory epithelium Small region in the nasal cavity that contains olfactory cells, basal cells, and supporting cells.

Olfactory gland Mucus-producing cell of the connective tissue underlying the olfactory epithelium.

Olfactory nerve Sensory nerve that runs from the nasal cavity to the olfactory bulbs.

Olfactory region Small yellow-tinged region in the nasal cavity containing 10 million to 20 million olfactory cells.

Olfactory tract Axons of mitral cells that transmit signals from olfactory bulbs to other parts of the brain.

Opsin Protein that combines with retinal to form visual pigment.

Optic disk Area in the retina where the optic nerve exits; also called the blind spot.

Optic nerve Nerve that carries impulses for the sense of sight.

Orbit Bony cavity in the frontal bone of the skull that holds and protects the eyeball.

Organ of Corti Receptor organ for the sense of hearing.

Osmoreceptor Cell that depolarizes in response to a loss of water by osmosis.

Ossicles The three small bones of the middle ear.

Otitis media A middle ear inflammation.

Otolith Tiny calcium carbonate crystals in the otolithic membrane.

Otolithic membrane Gelatinous membrane covering the hair cells of macula sacculi and macula utriculi.

Otosclerosis Loss of hearing due to overgrowth of bony tissue that fuses the stapes to the oval window or fuses the ossicles to one another.

Outer ear Portion of the ear composed of the external ear (auricle and lobule) and the external auditory canal.

Outer hair cell Cell that adjusts the response of the cochlea to different frequencies, which enables the inner hair cells to work with greater precision.

Outer segment Receptor region of a photoreceptor.

Oval window Oval-shaped aperture between the middle and inner ear into which the base of the stapes fits.

Pacinian corpuscle Phasic receptor located in the skin that senses deep pressure, stretch, tickle, and vibration.

Palpebral fissure The opening between the eyelids.

Perception Assigning meaning to a sensation based on experience.

Perilymph Fluid between the bony labyrinth and the membranous labyrinth of the inner ear.

Phantom pain Perception of feeling or pain in a limb after it has been surgically amputated.

Phasic receptors Receptors that generate a burst of activity when first stimulated, then quickly stop transmitting impulses even if the stimulus continues.

Phermone A chemical secreted by the body which travels through the air and can influence the physiology of another individual.

Photochemical reaction A reaction in which the chemical structure of a molecule is changed by interaction with light energy.

Photon Discrete unit of energy of light.

Photoreception Conversion of light energy to chemical energy by receptors in the retina of the eye.

Photoreceptor Receptor cell that responds to light energy.

Pigmented layer Outer, single-cell-thick layer of the sensory tunic.

Pitch The sense of whether a sound is high or low; determined by the frequency of sound waves.

Posterior cavity Large cavity behind the lens and ciliary body of the eye containing vitreous humor.

Posterior chamber Part of the anterior cavity located between the iris and lens.

Presbyopia Defect in vision resulting from advancing age that involves the loss of the ability of the lens to change its shape (accommodate), which inhibits close vision.

Proprioceptor Receptor located in skeletal muscles, tendons, and joints that is important for sensing the position and movements of the body and its parts.

Prostaglandins One of a group of fatty acids that are secreted by most body tissues and serve as sensory messengers.

Pupil The adjustable, central opening of the iris.

Pupillary reflex Constriction of the pupils in response to light illuminating the eyes.

Receptor potential Graded change in the voltage across a receptor cell membrane in response to a stimulus.

Receptor specificity The concept of receptors responding to specific kinds of stimuli.

Red cone Photoreceptor whose pigment responds maximally to wavelengths of light around 565 nm.

Referred pain Projection by the brain that may cause visceral pain to be perceived as somatic in origin.

Refraction Bending of light rays as they pass obliquely through media of different density.

Refractive index Measure of how much a medium refracts light rays relative to air.

Retina Inner layer of the sensory tunic that contains photoreceptors.

Retinal Light-absorbing molecule that is formed from vitamin A.

Retinal detachment Disorder characterized by separation of the retina from the pigmented layer, which allows the jelly-like vitreous humor to seep between them.

Retinopathy Disease of the retina.

Rhodopsin Visual pigment in the outer segment of retinal rods.

Rod Photoreceptor used for vision in dim light and for peripheral vision.

Root hair plexus Unencapsulated nerve ending that monitors the movement of hairs by wrapping around hair follicles.

Round window Membrane separating the middle ear from the inner ear.

Ruffini's corpuscle Tonic receptor for heavy touch, pressure, stretching of the skin, and joint movements.

Saccade Small, jerky movements that quickly move the eye from one location to another.

Saccule Anterior chamber of the vestibular apparatus used for sensing the position of the head in space.

Satiety center A region in the hypothalamus that leads to the sensation of fullness and satiation when stimulated.

Scala media Chamber of the cochlea located between the scala tympani and scala vestibuli that houses the organ of Corti; filled with endolymph.

Scala tympani Inferior chamber of the cochlea; filled with perilymph.

Scala vestibuli Superior chamber of the cochlea; filled with perilymph.

Scanning movements Eye movements that track an object that is moving.

Schwann cell Cell that forms insulation around nerve fibers.

Sclera Tough, white, fibrous tissue of the tunic fibrosa covering most of the outer surface of the eye.

Semicircular canal Bony canal in the temporal bone containing a semicircular duct.

Semicircular duct Structure of the vestibular apparatus that senses rotational movements of the head.

Sensation The awareness and localization of a stimulus.

Sense organ Localized collection of cells associated with a special sense.

Sensorineural deafness Loss of hearing due to damage of neural structures.

Sensory neuron A nerve that transmits signals from receptors to the central nervous system.

Sensory projection Ability to identify the site of stimulation based on information carried by nerve fibers.

Sensory reception Detection of stimulus energy by sensory receptor cells.

Sensory receptor Anatomical structure composed of sensory cells that is specialized to respond to specific changes in the environment.

Sensory tunic Innermost layer of the eye.

Serous glands Glands of the mouth that produce a thin, watery secretion.

Simple receptor Receptor composed of modified endings (dendrites) of a sensory nerve.

Slow pain A long-lasting, dull, diffuse feeling of pain following an injury.

Somatic pain Pain that arises from the skin, muscles, or joints.

Sound Any audible vibration of molecules.

Sound wave Series of pressure disturbances consisting of alternating compressions and rarefactions.

Special sense Any of the senses of hearing, balance, smell, vision, or taste.

Spectrum A band of colors seen when light is shown through a prism.

Stapedius A small muscle of the middle ear inserted into the stapes.

Stapes Middle ear bone resembling a stirrup in shape; attached to the oval window.

Static equilibrium Sensory information about one's position in space with respect to gravity.

Stereocilia Long, stiff microvilli on the surface of hair cells.

Stimulus A change in the internal or external environment that evokes a response.

Strabismus A disorder where the two eyes cannot focus on the same object.

Sty An inflammatory swelling of a sebaceous gland in the eyelid caused by a bacterial infection.

Supporting cell Cell in a taste bud that helps insulate sensory cells.

Suspensory ligament Ring of fibers attached to the ciliary body, which suspends the lens.

Tarsal plate A supporting connective tissue sheet in the eyelid.

Taste bud Sensory structure composed of specialized epithelial cells that mediate the sensation of taste.

Taste hairs Microvilli on the apical surface of taste cells.

Taste pore Fluid-filled space over a taste bud.

Tectorial membrane An anchored, gelatinous covering over the organ of Corti.

Tensor tympani A small muscle of the middle ear inserted into the malleus.

Thalamus An integrating, filtering, and relay center in the brain.

Thermoreceptor Receptor cell that responds to changes in temperature.

Thirst Desire for fluid, especially water.

Thirst center Region in the hypothalamus that leads to the sensation of thirst when stimulated.

Tinnitis A ringing or clicking sound in the ears in the absence of auditory stimuli.

Tonic receptors Receptors that adapt slowly and therefore generate nerve impulses continually.

Transduction Translation of a stimulus into an electrical signal by sensory receptor cells.

***trans*-retinal** The straight form of retinal induced by absorbing light.

Tunica fibrosa Outermost layer of the eyeball.

Tunica vasculosa Middle layer of the eye.

Tympanic cavity The indentation in the temporal bone that houses the structures of the middle ear.

Tympanic membrane A membrane separating the outer and middle ears; the eardrum.

Unencapsulated nerve endings General sensory receptors that are not wrapped in connective tissue.

Utricle Posterior chamber of the vestibular apparatus used for sensing the position of the head in space.

Vestibular apparatus Receptors for the sense of equilibrium located in the inner ear.

Vestibular membrane A membrane that separates the scala media from the scala vestibuli in the inner ear.

Visceral pain Pain from noxious stimulation of receptors in the organs of the thorax and abdominal cavity.

Visible light Region of the electromagnetic spectrum with wavelengths between about 400 and 700 nm.

Vision The perception of objects in the environment by means of the light they emit or reflect.

Visual acuity Measure of the resolving power of the eye rated against a standard in which a person with normal sight is considered to have 20/20 vision.

Visual pigment Photopigment in photoreceptors that changes shape when it absorbs light.

Vitreous humor Transparent jelly-like substance that fills the posterior chamber of the eye.

Volume depletion Fluid deficiency in which proportionate amounts of water and electrolytes are lost without replacement, such as during hemorrhage or chronic diarrhea.

Wavelength Distance between two consecutive wave crests (or troughs).

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Conversion Chart

Unit (metric)		Metric to English		English to Metric	
LENGTH					
Kilometer	km	1 km	0.62 mile (mi)	1 mile (mi)	1.609 km
Meter	m	1 m	3.28 feet (ft)	1 foot (ft)	0.305 m
Centimeter	cm	1 cm	0.394 inches (in)	1 inch (in)	2.54 cm
Millimeter	mm	1 mm	0.039 inches (in)	1 inch (in)	25.4 mm
Micrometer	µm				
WEIGHT (MASS)					
Kilogram	kg	1 kg	2.2 pounds (lbs)	1 pound (lbs)	0.454 kg
Gram	g	1 g	0.035 ounces (oz)	1 ounce (oz)	28.35 g
Milligram	mg				
Microgram	µg				
VOLUME					
Liter	L	1 L	1.06 quarts	1 gallon (gal)	3.785 L
				1 quart (qt)	0.94 L
				1 pint (pt)	0.47 L
Milliliter	mL or cc	1 mL	0.034 fluid ounce (fl oz)	1 fluid ounce (fl oz)	29.57 mL
Microliter	µL				
TEMPERATURE					
°C = 5/9 (°F – 32)		°F = 9/5 (°C + 32)			

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About the Author

Douglas B. Light is an accomplished educator who holds degrees in biology (B.A.), zoology (M.S.), and physiology (Ph.D.). His academic career began at Winslow High School in Maine, where he taught biology. He joined the faculty at Ripon College in Ripon, Wisconsin, in 1989 and taught general biology, anatomy and physiology, and immunology. He is presently professor of biology at Lake Forest College in Lake Forest, Illinois, where he teaches courses in organismal biology and animal physiology. He also conducts research designed to elucidate the mechanisms regulating transport of substances across biological membranes and how cells maintain their proper size. He has received more than half a dozen awards for his teaching and research excellence, and has been the recipient of several major grants from the National Science Foundation. He also has published more than a dozen articles in scientific journals, and has presented his research findings at numerous scientific conferences. Light is a member of several scientific and professional organizations, including the American Physiological Society, the Society for Integrative and Comparative Biology, and the Society of General Physiologists.